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# ZOÖLOGICAL BULLETIN

EDITED BY

C. O. WHITMAN AND W. M. WHEELER

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## CONTENTS OF VOL. II.

### ERRATA.

In No. 2, Vol. II, of this *Bulletin* the following corrections are to be made:

On page 83, line 21. In place of spino-occipital read occipito-spinal.

On page 84, line 4. In place of spino-occipital read occipito-spinal.

On page 85, lines 2, 6, 24, 26, 27, 32, 35. In place of spino-occipital read occipito-spinal.

	<i>The Embryology of the Apterygota . . .</i>	69-76
III. WM. E. RITTER.		
	<i>A Few Facts Concerning the Relationships and Reproduction of Some Bering Sea Tunicates . . . . .</i>	77-81
IV. EDWARD PHELPS ALLIS, JR.		
	<i>The Homologies of the Occipital and First Spinal Nerves of Amia and Teleosts . . .</i>	83-97





## CONTENTS OF VOL. II.

### No. 1. — July, 1898.

		PAGES
I.	ETHAN ALLEN ANDREWS. <i>Filose Activity in Metazoan Eggs . . . .</i>	1-13
II.	CHARLES B. WILSON. <i>Activities of Mesenchyme in Certain Larvae</i>	15-23
III.	O. P. HAY. <i>Observations on the Genus of Fossil Fishes called by Professor Cope, Porthenus, by Dr. Leidy, Xiphactinus . . . . .</i>	25-54

### No. 2. — October, 1898.

I.	HENRY LESLIE OSBORN. <i>Observations on the Anatomy of a Species of Platyaspis found Parasitic on the Uni- onidae of Lake Chautauqua . . . . .</i>	55-67
II.	AGNES M. CLAYPOLE, PH.D. <i>The Embryology of the Apterygota . . . .</i>	69-76
III.	WM. E. RITTER. <i>A Few Facts Concerning the Relationships and Reproduction of Some Bering Sea Tunicates . . . . .</i>	77-81
IV.	EDWARD PHELPS ALLIS, JR. <i>The Homologies of the Occipital and First Spinal Nerves of Amia and Teleosts . . .</i>	83-97

## No. 3. — December, 1898.

PAGES

- I. GEORGE WILLIAM HUNTER, JR.  
*Notes on the Finer Structure of the Nervous  
 System of Cynthia Partita* (Verrill) . . . 99-115
- II. ULRIC DAHLGREN.  
*The Maxillary and Mandibular Breathing  
 Valves of Teleost Fishes* . . . . . 117-124
- III. FLORENCE PEEBLES.  
*The Effect of Temperature on the Regener-  
 ation of Hydra* . . . . . 125-128
- IV. KATHARINE FOOT AND ELLA CHURCH STROBELL.  
*Further Notes on the Egg of Allolobophora  
 Foetida* . . . . . 129-150

## No. 4. — February, 1899.

- I. M. A. WILLCOX, PH.D.  
*Notes on the Occipital Region of the Trout,  
 Trutta Fario* . . . . . 151-154
- II. C. H. TURNER.  
*Notes on the Mushroom Bodies of the Inver-  
 tebrates. A Preliminary Paper on the  
 Comparative Study of the Arthropod and  
 Annelid Brain* . . . . . 155-160
- III. GUSTAV EISEN, PH.D.  
*Notes on North-American Earthworms of  
 the Genus Diplocardia* . . . . . 161-172
- IV. MAURICE A. BIGELOW.  
*Notes on the First Cleavage of Lepas* . . . 173-177
- V. CHARLES A. KOFOID.  
*On the Specific Identity of Cotylaspis In-  
 signis Leidy and Platyaspis Anodontae  
 Osborn* . . . . . 179-186
- VI. C. E. MCCLUNG.  
*A Peculiar Nuclear Element in the Male  
 Reproductive Cells of Insects* . . . . 187-197



## No. 5. — June, 1899.

PAGES

- I. C. H. TURNER.  
*A Male Erpetocypris Barbatus Forbes* . . . 199-202
- II. B. F. KINGSBURY.  
*The Reducing Divisions in the Spermatogenesis of Desmognathus Fusca* . . . 203-209
- III. MICHAEL F. GUYER.  
*Ovarian Structure in an Abnormal Pigeon* . . . 211-224
- IV. CHARLES W. HARGITT.  
*Some Interesting Egg Monstrosities* . . . 225-229
- V. E. C. CASE.  
*A Redescription of Pariotichus Incisivus Cope* . . . 231-245
- VI. HOWARD AYERS.  
*On the Pithecoïd Type of Ear in Man* . . . 247-250

## No. 6. — September, 1899.

- I. J. PLAYFAIR McMURRICH.  
*Contributions on the Morphology of the Actinozoa. V. The Mesenterial Filaments in Zoanthus Sociatus (Ellis)* . . . 251-273
- II. MINNIE MARIE ENTEMAN.  
*The Unpaired Ectodermal Structures of the Antennata* . . . 275-282
- III. GARRY DE NORD HOUGH, M.D.  
*Synopsis of the Calliphorinae of the United States* . . . 283-290
- IV. FRANK W. PICKEL.  
*The Accessory Bladders of the Testudinata* . . . 291-302





# ZOÖLOGICAL BULLETIN.

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## FILOSE ACTIVITY IN METAZOAN EGGS.

ETHAN ALLEN ANDREWS.

ONE who has not studied living Foraminifera or Radiolaria can get only an inadequate conception of the remarkable activities exhibited by the delicate protoplasmic extensions that form in such protozoans the thread-like pseudopodia. The figures and descriptions in text-books of zoölogy, in Verworn's *Physiology*, in Bütschli's *Protozoa*, or in special monographs naturally fall short of complete expression of the changeableness as well as the extreme delicacy of certain of these processes, though they teach us that the sensitive, contractile, coördinating powers of protoplasm may here be expressed in filaments of exceeding tenuity and inconstancy of form and position,—in flowing, liquid, apparently homogeneous protoplasm.

Such filose phenomena were practically unknown in Metazoa till a recent paper<sup>1</sup> described their occurrence in the eggs, polar bodies, blastulæ, gastrulæ, and larvæ of certain echinoderms. Here the cells put forth protoplasmic threads of excessive delicacy, that may branch and anastomose, elongate or shorten. By means of such filose processes the cells become connected amongst themselves, and, as these connections are living material comparable to the sensitive pseudopodia of many Protozoa, their importance in understanding the coördination of cells and their subordination to the entire mass, during the animals' development, was emphasized.<sup>1</sup>

Having been shown the filose threads in living starfish eggs, I have been able to observe the less attenuated ones present in

<sup>1</sup> Andrews, G. F., "Some Spinning Activities of Protoplasm in Starfish and Echinus Eggs," *Journ. of Morph.* Vol. xii. 1897.

the eggs of several other animals examined, and thus to extend the known occurrence of filose activities amongst Metazoa so widely that its importance seems strengthened and the probability of its still wider existence increased.

The first eggs examined, the frog's eggs in cleavage and gastrula stages, yielded when studied alive only the amœboid movement described by Roux; certain sections, however, showed intercellular connections that lead me to expect filose phenomena to be present here. A large number of sections of cleavage and larval stages in various frogs and in the salamander *Amblystoma punctatum* were carefully studied. In many sections of the latter animal, prepared and kindly loaned to me by Prof. C. B. Wilson of Westfield, Mass., as well as in certain frog's eggs, undoubted intercellular connections exist; but as their filose nature is not demonstrated, they will be but briefly noticed here. In the larva when the medullary folds are closed and the split mesoblast nearly fused on the ventral side, intercellular connections were seen between the large yolk cells, between mesoderm and mesenchyme cells, between the ectoderm cells on opposite sides of the nerve tube, between the ectoderm and mesoderm, and between the entoderm and mesoderm; in fact, cells in all germ layers and in each layer connect with those in another layer and with those in the same. Eliminating the deceitful appearances produced by coagulation of liquids between cells, by coagulation of fixative, by vacuolization and shrinkage of the superficial parts of cells, by the throwing off of pellicles, by the edges of drops and vesicles, and by fragments of vitelline membrane, as well as by scratches upon slide and cover glass, there still remained the above intercellular connections of undoubted protoplasm. These varied from fine filaments to broad bridges, and were either clear or contained some of the pigment granules of the egg. That they were filose in nature was indicated by their proportions and mode of origin and insertion; yet there was not decisive evidence that they were not produced in other ways either in the normal egg or in the egg when dying.

The next eggs, those of the annelid *Serpula*, were only examined alive and showed filaments passing out from the surface of the egg toward and to the membrane, both before and after the



first cleavage, as elsewhere mentioned.<sup>1</sup> Later, in the gastrula stage, filaments were seen passing from the ectoderm to the membrane. However, no undoubted case of filaments connecting cells was observed in the comparatively few eggs studied.

The eggs of a nudibranch mollusk, *Tergipes despectus* (?), were examined alive at a later date, and showed similar filose phenomena. In an egg not yet divided and having one polar body formed, numerous fine filose threads were seen projecting from the surface into the wide space between egg and membrane. Most of these filaments were confined to one quarter of the periphery, as seen in optical section; but one isolated, blunt, branched process came up some distance from the others near the polar bodies, which were of unequal lengths, a few longer ones reaching out halfway to the membrane. The longer ones often showed short branches at the tip and swellings along their length, suggesting those on the pseudopodia of filose Protozoa. Moreover, a vibrating particle beyond the finest filaments, and scarce seen with ocs. 6 and 8 and obj. 2 mm., moved out and then back again toward the egg, as if it might have been traveling upon some finer filament not seen.

The early stages of several marine lamellibranchs were very briefly examined. In *Yoldia limatula* an egg before dividing was seen to send out innumerable fine filaments from a thin layer of waving ectosarc. As these filaments were crowded together and radiated directly outward, they looked not unlike the cilia the larva developed, but they were much finer. These filaments did not spring from the entire surface of the egg, but from large areas. At one point a comparatively coarse process, suggesting an icicle in high refractive power and shape, projected amidst the finer filaments. As there was no membrane, all these filose processes projected freely into the sea water.

Again, in a much more prolonged study of the eggs of the large nemertean worm *Cerebratulus lacteus* Verrill, certain filose phenomena were seen before and after the first cleavage. The pear-shaped egg removed from the female had a more or less pronounced prolongation at its pointed pole. From this pro-

<sup>1</sup> Andrews, E. A., "Spinning in *Serpula* Eggs," *American Naturalist*. September, 1897.

longation fine filaments were seen to radiate in all directions and to rapidly change, and in other cases comparatively blunt filaments occupied the same place. Before this prolongation was drawn into the main mass, many fine filaments appeared from the opposite blunt end of the egg. As it was being drawn in, fine, short filaments were seen projecting from the surface of the egg round about its base. Under oc. 12, obj. 2 mm., these were much finer than the tail of the large sperms now often present within the egg membrane. When the polar bodies were forming, and for a time after their extrusion, the surface of the egg near these bodies (and sometimes quite generally) sent out very fine filaments, set like cilia close together.

Later, during the first cleavage, similar filaments arose from the surface of the egg. They were especially well seen when occurring as stout, stiff-looking, radiating lines arising from the tops of certain remarkable papillæ that frequently formed on the sides of the gaping cleavage furrow. As these small papillæ armed with tufts of filose processes arose at certain phases in cleavage and then vanished, they suggested some such temporary interconnection of cells as occurs in certain echinoderms;<sup>1</sup> but the filaments could not be followed from one cell to the other and seemed much too short to furnish any intercellular union by filose activity. In this connection it seems significant that the cleavage is of such a nature as to leave it doubtful, from surface views, whether the blastomeres actually separate entirely as in the echinoderms, or not.

In an egg with twenty or more cells fine processes were seen projecting from the profile of a cell favorably placed. In another case, where there were but four cells, a stout filament passed across the space between the inner ends of the cells, near the surface, and made the protoplasm of two opposite cells continuous. On this filamentous bridge there were nodular enlargements that gradually grew smaller as the filament dwindled in diameter and was withdrawn into one of the cells. But as the mode of formation of this connecting filament was not observed, and as the egg subsequently showed abnormal

<sup>1</sup> Andrews, G. F., "Some Spinning Activities of Protoplasm in Starfish and Echinus Eggs," *Journ. of Morph.* Vol. xii. 1897.

features, this was decided not to be a case of filose activity. In the same egg some shorter, slender pseudopodia projected from one cell, but could not be traced more than a tenth of the distance to the opposite cell toward which they extended over the above-mentioned polar space.

The most delicate filose displays were seen near the polar bodies during the first and second cleavages. The egg put forth fine protoplasmic threads that branched and reached up toward the second polar body. In this region a sheet of substance connected the egg with the second polar body, and the filose phenomena in it led to the assumption that it was a flowing mass of protoplasm, or that it contained more or less of it. But this, with the remarkable filose activities of the polar bodies, has been described and figured elsewhere.<sup>1</sup> In both a gastropod and a lamellibranch, the polar bodies were likewise seen to have filose activities.<sup>2</sup> Thus in several great groups of animals the polar bodies may act in a filose way for some time after their extrusion, plainly exhibiting contractile phenomena in their cytoplasm and showing themselves to be still alive and active, so that, whatever may be their import as regards the chromatin they carry with them, they appear as more or less isolated parts of the egg mass, carrying on filose changes of the same nature as those of its other parts.

Being convinced that filose phenomena essentially similar to those of certain Protozoa exist also in the great metazoan groups Echinodermata, Annelida, Mollusca, and Nemertina, another attempt was made to find them in Chordata by studying some preserved *Amphioxus* eggs. However, the relation between living and preserved material is so remote in cases of such delicate phenomena as these sought, that little weight could be laid upon the results without a knowledge of the live eggs. Lacking this, it was thought that an acquaintance with the live and the preserved eggs of echinoderms would suffice to enable one to draw tentative conclusions from the preserved

<sup>1</sup> Andrews, E. A., "Activities of the Polar Bodies of *Cerebratulus*," *Archiv. f. Entwicklungsmechanik*. Bd. vi. 1898.

<sup>2</sup> Andrews, E. A., "Some Activities of Polar Bodies," *Johns Hopkins University Circulars*. Vol. xvii, No. 132. November, 1897.



Amphioxus eggs. The following three figures illustrate some of the appearances seen in live and in preserved echinoderm eggs, and may aid in justifying the conclusions formed as to the nature of the intercellular connections found in *Amphioxus*.



FIG. 1.

Fig. 1 represents a small part of a blastula of the starfish common at Roscoff, France, and is reduced one-half from a camera sketch made by G. F. Andrews in 1894 with oc. 8, obj. 2 mm., tube 170 mm. A small opening into the blastula is seen, surrounded by cells that are actively spinning out fine filaments by means of which they are variously connected with one another and with the two polar bodies. These lie, in this case, in the opening or cleavage pore, and are temporarily connected to adjacent cells while giving off very remarkable dendritic pseudopodia, along which protoplasm flows and collects in lumps. The chromosomes are not shown in the polar bodies,

nor in the enlargements on their pseudopodia, into which they were sometimes carried; vacuoles, however, are indicated in the main part of each polar body. The short, apparently blunt filaments projecting from the edge of the cell uppermost in the

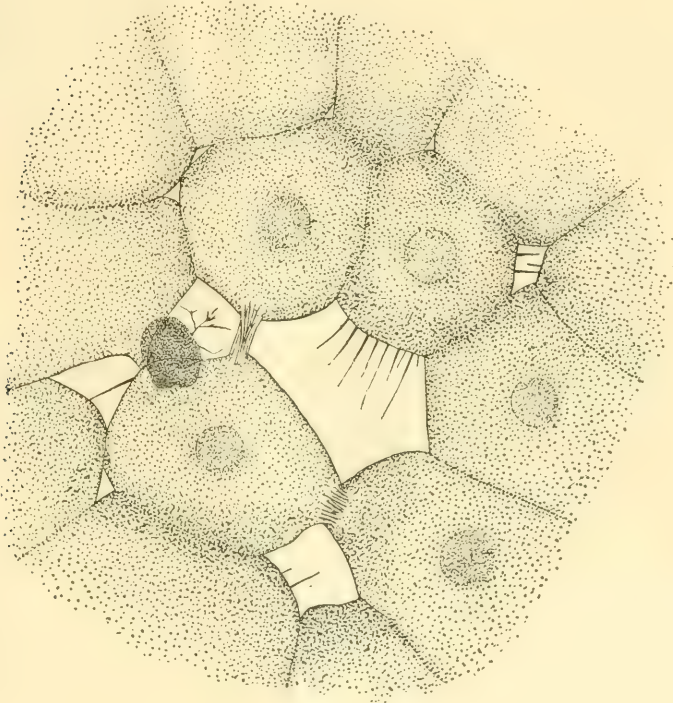


FIG. 2.

figure really represent threads that bent abruptly and extended far inward, and were, in most cases, attached to distant cells of the blastula.

This opening into the blastula closes in with change in position of the adjacent cells, and with changes in the character of the filose activities that lead one to conclude they are instrumental in associating the cells more intimately. Thus in Fig. 2 a later stage shows the cleavage pore reduced to a few small chinks between the cells that have glided over it. The polar bodies were here taken inside, and are represented, lying one over the other, by the black mass to the left.

In the lower part of the figure a cell to the left has reached out over one to the right and established a connection with it by means of a broad strand of filaments. An earlier stage of a similar process is shown above, where the same left cell is strongly bound to an upper cell by double strands of filaments. These filaments seem instrumental in drawing the cells together to cover in the cleavage pore. This figure is reduced one-half

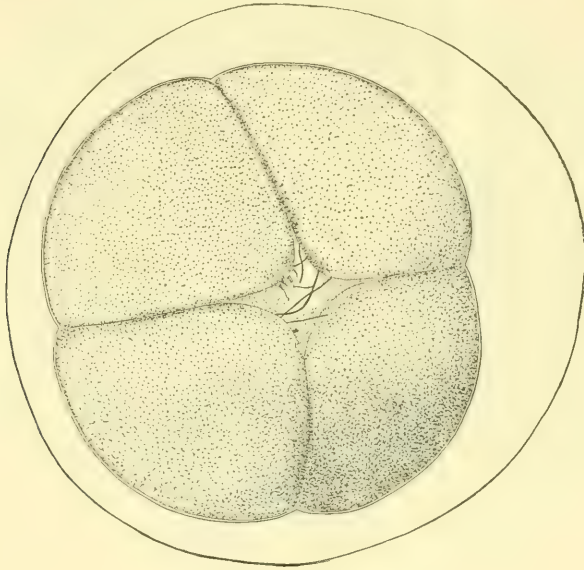


FIG. 3.

and otherwise like the first in execution, except that it was drawn with oc. 6.

In both these figures the thickness of the finer filaments is exaggerated in drawing, and hence they do not adequately indicate the delicacy of these processes. Moreover, as they are constantly changing, and as they contract and draw in when stimulated by certain chemicals or even by mechanical insult to the egg, it is plain that usual methods of preservation will fix but part of these displays, at the most, and that they may be readily broken off in subsequent treatment. However, it was found possible to preserve some of the larger filaments or amalgamations of filaments by special methods, and intercellular



connections and other spinnings have been retained, both in starfish and in sea-urchin eggs for three years.

Thus in Fig. 3 a four-cell stage in the common echinus of Roscoff shows filaments passing from cell to cell. These are drawn considerably thicker than the actual threads seen, but otherwise represent them truly. The figure is a surface view camera drawing with oc. 8, obj. 2 mm., tube 160 mm., helped

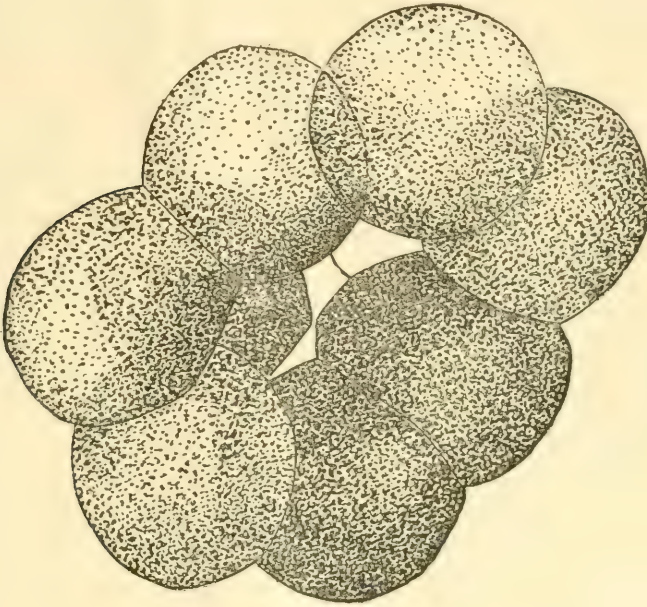


FIG. 4.

out with ocs. 12 and 18. On the left, above, a series of elevations from one cell seemed to be the remnants of tufts of filaments, while the granular matter, imperfectly represented here, partly covering the cleavage pore, appeared to be the same as Hammar's ectoplasmic layer.<sup>1</sup>

There can be no doubt that these filamentous intercellular connections are the preserved remnants of the active filose threads of the living egg.

Some eggs of *Amphioxus* killed in corrosive acetic and stained in Orth's new lithium carmine, as well as some killed

<sup>1</sup> Andrews, E. A., "Hammar's Ectoplasmic Layer," *American Naturalist*, December, 1897.

in Flemming's fluid and not stained, were kindly placed at my disposal by Professor T. H. Morgan. Both those mounted in balsam and those studied in alcohol showed undoubted filaments connecting the blastomeres in various cleavage stages. From the resemblance of these filaments to those found in preserved echinoderm material there seemed little doubt that this was probably another case of filose intercellular connections, but there must remain some doubt till the live egg is studied. In living material we may expect to find filose displays as remarkable as those in the echinoderms, and, in part at least, more readily observed.

In four, eight, and sixteen-cell stages, many eggs showed such marked intercellular connections as the one represented in Fig. 4. These filaments are of clear material that arises from the clear ectosarc of one cell and becomes continuous with that of another cell. Only a few cases of branching were seen, apparently only the main trunks and grosser threads being preserved.

Fig. 4 shows an eight-cell stage in *Amphioxus*, with a definite abruptly curved filament passing from one cell to an opposite one at the bottom of an open cleavage cavity. This is from a camera sketch with oc. 2 and obj. D, not reduced. One cell showed a marked elongation toward another, but no connecting filaments were seen, though they may well have existed there in the live state. Besides the filaments seen connecting cells, as in the above figure, there were other signs of filose activity in these eggs; groups of minute spherules and filaments protruded from the ectosarc as if remnants of filose processes. There were also large ectosarcular outflows near cleavage planes, suggesting the amoeboid elevations described for the eggs of certain nematodes by Erlanger.<sup>1</sup>

When more highly magnified these intercellular filaments in *Amphioxus* appear as in Fig. 5, which represents part of another eight-cell stage, drawn with camera, oc. 8 and obj.  $\frac{1}{12}$  in. Here a filament arose from the ectosarc of one cell, and, after making a complex bend, difficult to understand, gradually dwindled in diameter till it became continuous with the surface of another

<sup>1</sup> *Biol. Centrblt.* Bd. xvii. 1897

cell on the opposite side of a narrow cleavage space at the center of the rather compact group of eight cells.

Such intercellular connections as this would seem to be, in all probability, of the same nature as those seen in live and in preserved echinoderm eggs. And if such be the case, it is especially interesting to find them in *Amphioxus*, not only as this is in many respects so diagrammatic a representative of the Chordata as to lead one to infer its filose phenomena will

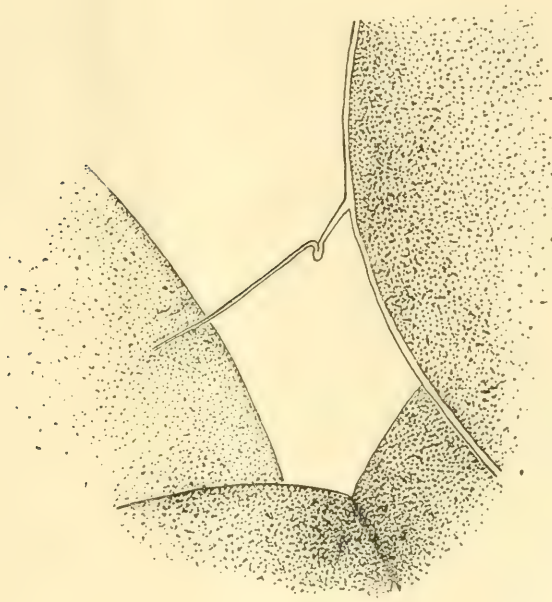


FIG 5.

be found, in modified form, in various vertebrates, but because the egg of *Amphioxus* has been so carefully studied by experimental methods that the need of an organic intercellular connection to explain known facts in embryology is here especially felt. Thus Prof. E. B. Wilson was led to conclude in his study of *Amphioxus*,<sup>1</sup> "*that the unity of the normal embryo is not caused by a mere juxtaposition of the cells. . . . This unity is not mechanical, but physiological. . . . There must be a struc-*

<sup>1</sup>"*Amphioxus and the Mosaic Theory of Development,*" *Journ. of Morph.* Vol. viii. 1893.



*tural continuity from cell to cell that is the medium of coördination, and that is broken by mechanical displacements of the blastomeres."*

The nature of this structural continuity was not surmised, but it now seems evident that it is really, in part at least, brought about by such remarkable, changing, pseudopodial threads as were seen in the echinoderms and preserved, in part, in the *Amphioxus* eggs I had for examination.

That filose phenomena will be found in the blastula and gastrula stages seems most probable, but as yet I have not been able to find remnants of them in the above-preserved material. The figures published by Klaatsch<sup>1</sup> in illustration of other problems suggest, at first sight, profuse intercellular connections in these stages of *Amphioxus*, but it seems more probable that the lines there shown are the results of shrinkage and imperfect preservation, though some filose activity may have furnished an element for certain of the distortions that resulted.

As filose phenomena in eggs as far as yet studied are, to say the least, easily overlooked (in the echinoderms, they can be seen only with difficulty, though the main threads from the polar bodies of *Cerebratulus* and the above connections in *Amphioxus* are so distinct as to be readily evident with low powers to one searching for them), we need not expect to find them frequently mentioned in the past literature of embryology. Yet some of them must have been seen, even if passed by as of little moment. Thus Professor Conn described and figured<sup>2</sup> fine lines passing out from the surface of the egg of the geophyrean worm *Thalassema mellita* Conn to the rather distant membrane. These he regarded as striæ and interpreted as indicative of the presence of a jelly-like substance between egg and membrane. Yet an examination of his Fig. 13, Pl. XX, suggests that this egg and its polar bodies will prove to possess filose phenomena.<sup>3</sup>

<sup>1</sup> "Bemerkungen über die Gastrula des *Amphioxus*," *Morph. Jahrb.* Bd. xxv, 1897. Pl. XII.

<sup>2</sup> Studies from the Biological Laboratory, Johns Hopkins University. Vol. ii. 1884.

<sup>3</sup> In correcting proof I add that the connection made by Professor Flemming (*Merkel and Bonnet, Ergebnisse*, 1897, p. 279) between certain fine pseudopodia-

*Conclusions.*

Filose activities like those of the finer pseudopodial threads of certain Protozoa were seen in the living eggs of Metazoa, in Echinodermata, Annelida, Mollusca, and Nemertina. Study of preserved material makes most probable their existence in *Amphioxus* and quite probable their existence in *Amphibia*. Members of other great groups have not as yet been examined from this point of view.<sup>1</sup>

Such filose filaments connect the cells in the eggs and larvæ of Echinodermata; filaments that are most probably of this nature connect the blastomeres of *Amphioxus*; filaments probably filose connect the cells in eggs and larvæ of *Amphibia*.

Wherever found, filose connecting filaments may be assumed to have the importance ascribed to them on their first discovery in the echinoderms, and to furnish a medium for coördinating the activities of parts of the embryo.

JOHNS HOPKINS UNIVERSITY, BALTIMORE,  
January 29, 1898.

like lines seen by him on a polar body of *Anodonta* in 1873 (*Archiv. f. mikr. Anat.*, Bd. x) and the filose phenomena of Echinodermata as described by G. F. Andrews seems to me probably correct.

<sup>1</sup> However, at this later date, March 7, I am able to state that the cleaving eggs of a green *Hydra* have remarkable ectosarcial displays and some interconnection of cells by filose activities; this in addition to the gross pseudopodia described by Kleinenberg.





## ACTIVITIES OF MESENCHYME IN CERTAIN LARVAE.

CHARLES B. WILSON.

IN consideration of the attention which has recently been given to a study of the phenomena of the living cell, the following observations may be found of some interest. They were made during the summers of 1896 and 1897 upon mesenchyme cells in the larvae of certain species of molluscs and nemerteans.

Freshly laid eggs of the nudibranch mollusc *Tergipes despectus* (?) were obtained and reared to the veliger stage. Both egg and young embryo are nearly opaque, the gastrula invagination being distinguished only by a slight increase in the density. But after the mantle has been formed and the shell has been secreted, the veliger becomes perfectly transparent. The delicate shell is as clear as the finest glass, and the whole internal structure is now plainly visible.

Mesenchyme cells appear very early in development. They arise from large primitive endoderm cells at the posterior edge of the blastopore in the ordinary way for gastropod molluscs, and are set free in the segmentation cavity. At first they are approximately spherical in shape, and float about freely in the liquid which fills the cavity, but they soon begin to elongate, and become spindle-shaped. At this stage in their development activities were observed which are probably analogous to those described for the polar bodies of certain animals.<sup>1</sup>

Unfortunately, I did not have with me at the time an objective of sufficient power to bring out the finer protoplasmic movements distinctly. Well-defined amoeboid changes of outline, however, could be plainly seen. The cell, as it moves about in the liquid which fills the segmentation cavity, puts out blunt pseudopodia-like processes. These change both their

<sup>1</sup> Andrews, E. A., "Some Activities of Polar Bodies," *Johns Hopkins University Circular*. November, 1897.

shape and position. There seems to be a special tendency to their formation whenever the cell comes close to the wall of the cavity, or when two cells approach each other. The processes remain short and blunt, and in no instance were they seen to reach either the wall or a neighboring cell. The putting out of these processes was seen to be accompanied in several instances by corresponding movements of the cell contents very similar to those in an amoeba.

Certain disturbances were also noticed in the liquid close to the surface of the cell. At the time these were considered analogous to slow ciliary motion, and they were probably caused by "filose" action.

It was impossible to determine with certainty whether the amoeboid changes ceased and were followed by a period of rest before the cell became permanently branched; but this would seem probable from analogy.

At all events, permanent processes soon appear, the cells become fastened in place, and after subsequent development function as muscles.

During the development, after the cells become branched, certain activities appear which are of an entirely different nature.

A single cell, or more often a pair of these mesenchyme cells, may be found in close proximity to the internal wall of the mantle on one (usually the right) side nearly in the center (Fig. 1).

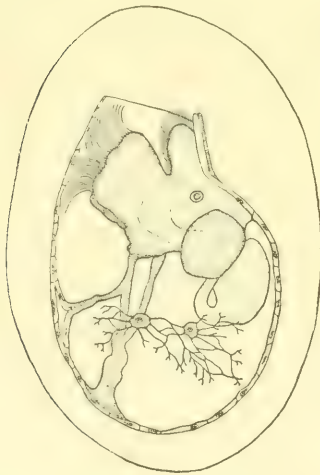


FIG. 1. —Side view of veliger larva of *Terigipes*, showing position of the two contractile cells. Cam. luc. drawing, Leitz objective No. 3, Eye-piece No. 3.

These two cells are in close proximity to each other, and each consists of a body and radiating branches. The body is composed of finely granular protoplasm, and contains a distinct nucleus and several vacuoles. From it branches extend in many different directions. There are usually several fine branches reaching directly across from the body of one cell to

that of the other, which serve to bind the cells firmly together. The other branches are at first of about the same size, but one branch from each cell, extending outward (*i.e.*, away from the twin cell), becomes very quickly larger than the rest, sometimes approaching the diameter of the cell itself. These two larger branches are seldom in the same straight line, but usually make a more or less obtuse angle with each other. That they are really branches and not simply a prolongation of the cell body is apparent from the fact that they are finely fibrous in structure like all the other branches, and not granular like the body of the cell.

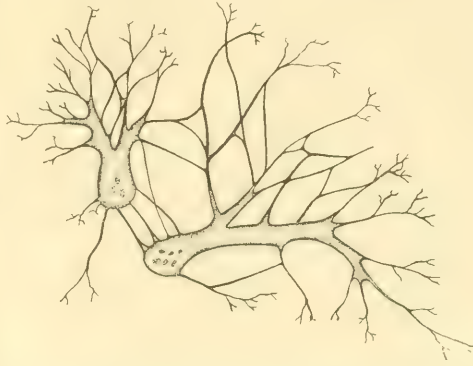


FIG. 2.—The two contractile cells enlarged to show their structure. Cells relaxed. Cam. luc. drawing, Leitz objective No. 7, Eye-piece No. 3.

These large branches extend some distance from the cell and then divide dichotomously, ending in fine fibrils.

The smaller divisions of these branches, together with those of the cell itself, anastomose freely and form a loose reticular network. These details of structure appear to better advantage in the enlarged drawing of the two cells shown in Fig. 2.

At this stage of their development they are not attached to anything except to each other, but the network formed by their interlacing branches extends over a considerable area and holds them in position.

They appear like ordinary mesenchyme cells, but upon being watched they are seen to possess a peculiar contractile power, which is manifested at intervals. In a few individuals the contractions occurred at definite intervals as long as the cell was watched, but more frequently there was a period of rest after a few contractions. Both the time of contracting and the intervals of rest were subject to considerable variation, but the latter was never long enough to enable a camera lucida sketch

to be made. The drawings in Figs. 1 and 2 were taken from individuals which had been paralyzed with magnesium sulphate.

These cells are isolated from everything except the liquid in which they lie, and, consequently, if there be any stimulus previous to contraction, it must be given through the medium of the liquid or it must arise spontaneously in the cell itself.

By careful watching, the contraction can be seen to begin in the cell body and travel outward along the branches, though the contractile wave moves so quickly that it practically begins at all points simultaneously. As a result of its action the protoplasm draws together, the cell body becomes more spherical, all the branches, large and small alike, become shorter and thicker, and the whole meshwork of fibrils is drawn in until it occupies much less area than formerly.

When it first begins, the contraction is comparatively weak and results simply in a shortening of the branches and fibrils, but as it proceeds it becomes rapidly stronger and stronger. This increase in contraction cannot manifest itself in any further shortening of the branches, for they have already

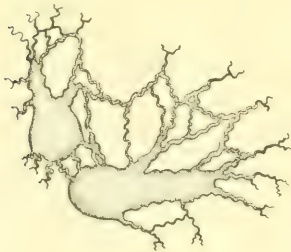


FIG. 3. — The same two cells at the close of contraction. Leitz objective No. 7, Eye-piece No. 3.

shortened all they are capable of doing. The only way in which the two ends of any branch can now be brought nearer together is by a bending or folding of the fibers upon themselves, and this is what actually occurs. At the close of contraction (Fig. 3) the smaller branches and fibrils have been drawn in so much that they are twisted into a corkscrew shape for their entire length. The large branches have also contracted so strongly that their surface becomes wavy or sinuous in outline. The bodies of the cells remain spherical, but become so opaque that neither nucleus nor vacuoles are visible.

This twisting or plication of the muscle fibers, whereby their retractive power is increased, is also shown in the retractor muscle of the velum (Fig. 1), and will be noticed later in certain muscles of the nemertean larva. The same thing has



been observed in "single fibrils in protoplasm, as well as contractile pellicles and substance membranes," and also in Metazoan cilia and the muscle bands in rotifers.<sup>1</sup> It seems to be carried farther here than in the muscles mentioned, for the simple reason that these filaments are unattached and, therefore, there is nothing to restrain it.

After remaining an instant in this extreme contraction, the cells relax, and the return to a normal condition is practically instantaneous. We have here, then, the same power manifested by the single mesenchyme cell, with its branches, that belongs to the more complicated retractor muscle, and that, too, when it is isolated from everything save the liquid in which it floats.

This must certainly be a very near approach to a primitive muscular contractility.

The contraction lasts one and a half or two seconds, the relaxation occupies but a very small fraction of a second, while the pause or rest varies from two or three to twelve or fifteen seconds. This suggests very forcibly a condition similar to that which obtains in the beating of the heart, with the exception that in these mesenchyme cells the relative duration of contraction and relaxation is reversed, the former being much longer.

This same contractile power is also possessed, to a less degree, by the other mesenchyme cells. They may often be seen to contract after they have become branched. The contractions are not as rhythmical as those just described, but they are as automatic. Some of these mesenchyme cells enter the velum during development and become attached to its walls until the whole interior is traversed from wall to wall by their branches, rendering it highly contractile.<sup>2</sup>

In this case, therefore, the same cell which contracts at first automatically may afterward become a part of the muscular network of the velum, where it is under the control of the central nervous system.

Similar phenomena were observed in the mesenchyme cells of the pilidium larvae of the Nemertean *Cerebratulus lacteus*

<sup>1</sup> Andrews, G. F., *The Living Substance as Such: and as Organism*, p. 103. 1897.

<sup>2</sup> Lang, *Comparative Anatomy*, Part II, p. 257.

Verrill. These larvae were reared from artificially fertilized eggs, and a full account of their development is in preparation for a subsequent paper. The eggs of this nemertean are opaque during cleavage and gastrulation, but become beautifully transparent on reaching the pilidium stage.

The mesenchyme first appears as isolated cells derived from the ectoderm, as observed by Metschnikoff (*Zeit. f. wiss. Zool.*, Bd. xxxix).

They move about freely in the gelatinous liquid which fills the space between ectoderm and entoderm. At first they are nearly spherical in outline, but they soon begin to develop processes and become branched, in which condition they are very readily distinguished from the other elements. So long as they remain free floating there is no indication of cell fibers, but simply a nucleus enclosed in cytoplasm. But as they begin to branch they grow larger, and granules appear in the cytoplasm, while the branches become gradually fibrous in structure. No amitotic division stages, however, were noticed in any of these cells, such as were found by Montgomery in the free-floating mesenchyme cells of the adult worm (*Zool. Jahrb.*, Bd. x). The branches hinder the freedom of motion of the cells, and the latter gradually become fixed in position.

The fibrils at the extremities of the branches are then fastened in place, and from being mere wandering mesenchyme the cell becomes one of the muscles of the pilidium. This transformation was watched several times in the formation of different muscles, and nearly all the intermediate stages were observed. The most important muscle of the pilidium is the one which extends from the apical plate downward to the anterior border of the lappets. The development of this muscle was watched in many different individuals. When the mesenchyme cells first develop branches, one of them can be seen to become stationary in about the position of the future apical muscle. One of its processes becomes fastened to the apical plate, while another fastens to the wall of the digestive tract, and sometimes a third connects with the aboral wall of the pilidium (Fig. 4). The number of processes is not constant, but the position assumed by the cell is approximately so.

Other cells become fastened to the walls of the digestive tract along its anterior border. The branches of these cells anastomose with each other and with the first cell, and from them are developed the strong muscle which enables the larva to retract the apical plate with its tuft of cilia. This muscle becomes attached at first to the wall of the digestive tract, as figured by Verrill (*Marine Nemerteans of New England*, p. 417). But as soon as the branches begin to anastomose it

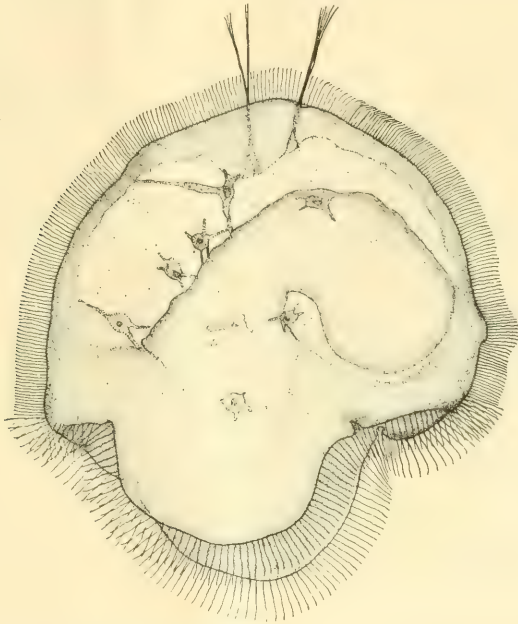


FIG. 4. — Side view of pilidium larva, showing mesenchyme cells in position to form the apical muscle. Zeiss cam. luc.  $\times 575$  diams.

develops along the line of mesenchyme cells seen in Fig. 4, and becomes fastened to the anterior border of the lappets. In a similar way a transverse muscle is formed just in front of the apical plate.

This consists of a single large mesenchyme cell which subsequently develops long processes reaching from one side of the pilidium to the other. In later development the whole internal surface of the umbrella is covered with a loose meshwork of anastomosed mesenchyme cells, which give the larva so much

contractile power that it frequently tears the umbrella cells apart by violent contractions when irritated.

While floating about freely these mesenchyme cells do not contract, so far as could be observed, but as soon as they begin to form processes they can be seen to contract. Occasionally two cells anastomose with each other before becoming attached to the wall of the pilidium.

In such a case they contract irregularly at first, the intervals between contractions being unequal, but later the contractions become rhythmical and very closely resemble those of the opisthobranch gastropods just described. Three or four contractions occur in rapid succession and are followed by a comparatively long rest. After the cell branches become fastened to the pilidium wall these rhythmical pulsations cease. The mesenchyme cells now become regular muscles of the larva and contract only when stimulated from the central nervous system.

We are witnessing here, then, the passage from an automatic condition, in which the cells contract quite independently from the rest of the larva, into a condition in which every contraction is definitely correlated with that of the other larval muscles.

In this nemertean larva the intense contractions resulting in a corkscrew shortening of the branches and fibers occurred subsequent to the fixation of the cells. It was not noticed in any of the free cells even when two of them anastomosed before becoming attached, and all the conditions appeared as favorable as in the veliger larvae. After attachment such a shortening is very noticeable, especially in the apical muscle and the fine radial muscles of the side lappets.

In an examination of these larvae, therefore, it is found that:

1. The mesenchyme cells are at first nearly spherical and are free-floating. In this condition they consist simply of a nucleus and cytoplasm; they may put out amoeboid processes, but they do not show any contractile movements.

2. They soon grow larger, become granular, and develop fibrous branches which hinder their free motion, and finally they become fixed in position and function as muscles.



3. In both larvae prior to such fixation cells may be found, singly or in pairs, which pulsate in more or less rhythmical contractions until their branches become fastened to the larval tissue, when the pulsations cease.

4. Both larvae, accordingly, show a well-marked transition from automatic pulsations to muscular contractions dependent upon the central nervous system.

STATE NORMAL SCHOOL, WESTFIELD, MASS.,  
April 18, 1898.



OBSERVATIONS ON THE GENUS OF FOSSIL  
FISHES CALLED BY PROFESSOR COPE,  
PORTHEUS, BY DR. LEIDY,  
XIPHACTINUS.

O. P. HAY.

THE earliest reference which we have to any remains of the genus of fishes usually called *Portheus* is that found in Mantell's *Geology of Sussex*, p. 241, Pl. XLII, 1822. No systematic name is there assigned to this fish. Later, Louis Agassiz, in his *Poissons Fossiles*, vol. v, p. 99, referred to Mantell's description, and refigured the materials (*op. cit.*, Pl. XXV *b*, Figs. 1 *a*, 16), presenting at the same time additional figures of remains from the same locality (Pl. XXV *a*, Fig. 3 ; Pl. XXV *b*, Figs. 2, 3). All these he included, with other remains, under the name *Hypsodon lewesiensis*.

In 1871, in *Proc. Amer. Philos. Soc.*, vol. xii, p. 175, Professor Cope established the genus *Portheus*, founding it on materials collected in the cretaceous deposits of Western Kansas. The type of the genus was called *Portheus molossus*. Later, in the same volume, p. 330, Cope recognized the affinity of the remains figured by Agassiz, as above cited, to those of *Portheus*, as well as the fact that other remains had been included by Agassiz under the term *Hypsodon* which were not congeneric with *Portheus*. Professor Cope, therefore, restricted *Hypsodon* to those bones and teeth which differed generically from his own American materials, and included the remainder under *Portheus*. In this same paper, pp. 333, 335, Cope also referred to *Portheus* a species which he had described in 1870 (*Proc. Amer. Philos. Soc.*, vol. xi, p. 533) under the name of *Saurocephalus thaumas*. Both these species and others were fully described in his *Cretaceous Vertebrates*, published in 1875.

At this point it may be noted that in the year 1870 (*Proc. Acad. Nat. Sci. Phila.*, p. 12) Dr. Joseph Leidy described from the Cretaceous of Kansas the spine of a fish which he called

*Xiphactinus audax*, and which, without doubt, belongs to the Saurocephalidae. A more complete description and figures of this fossil spine were given by Dr. Leidy in his *Contributions to the Extinct Vertebrate Fauna of the Western Territories*, p. 290, Pl. XVII, Figs. 9, 10. This was published in 1873.

Professor Cope first recognized the affinities of this spine in a paper in Hayden's *Second Annual Report of the Geological and Geographical Survey of the Territories*, 1871, p. 418, where he assigned it to the genus *Saurocephalus*, in which genus he also arranged the species which he later called *Portheus thau-mas*. He compares the spine with one obtained from *S. prognathus*, a fish which he later relegated to the genus *Ichthyodectes*, itself a close relative of *Portheus*. From about this period up to 1874 Professor Cope held the opinion that certain fin remains belonged to *Portheus*, and probably to the pectoral fin, which it is now pretty certain belong to *Protosphyraena*. Other spine-like fin rays, whose resemblance to Leidy's *Xiphactinus* he admitted, he regarded as also belonging to *Portheus*, and probably to the ventral fins. He claimed, however, that *Xiphactinus* was distinct from both *Portheus* and *Ichthyodectes*; but he does not specify the points of difference. By the time of the publication of his *Cretaceous Vertebrates* in 1875, he had become convinced that the fin structures which are now assigned to *Protosphyraena* did not belong to *Portheus*; and to them he gave the name *Pelecopterus*. He had also learned that the ventral spine-like fin rays of his *Portheus* did not differ greatly from those of the pectoral fin (p. 204). Of *Xiphactinus* he says: "Dr. Leidy applied the name *Xiphactinus* to a genus indicated by a spine in some degree like those regarded above as ventrals of *Saurodontidae*. Whether it belongs to any of the genera above enumerated, or, if so, which of them, is a question which can only be settled by future investigation" (*op. cit.*, p. 190).

Accompanying a considerable collection of specimens of *Portheus* collected for me in Western Kansas, in the region of Butte Creek, are many large spines, some nearly complete, others in fragments. Some of these belong to the shoulder girdle which I have figured (Fig. 9), and this, I have no doubt, belongs to



Cope's genus *Portheus*. No more doubt exists in my mind regarding the generic identity of many of the other spines. Some of these, indeed, were found in a block of soft limestone, and were in close relation to jaws, vertebrae, etc., of *P. thau-mas*. These spines I have compared with Leidy's type of *Xiphactinus audax*, and I find no difference that can be regarded as generic. Both Cope, in his *Cretaceous Vertebrates*, and Crook, in *Palacontographica*, vol. xxxix, p. 119, have described and figured spines of *Portheus* which differ in no essential respect from *Xiphactinus*. The genus *Ichthyodectes* possessed pectoral spines not greatly different in structure from those of *Portheus*; but none of them attain the size of those assigned to *Xiphactinus* and *Portheus*. Taking all the facts into consideration, it seems to me that there can be no reasonable doubt that *Xiphactinus* is the same as *Portheus*, and ought to supersede it as a name for this genus of fishes. It is quite probable that *X. audax* is the same as some one of Professor Cope's species of *Portheus*; but it will require a careful study of well-identified spines of all the species, and a comparison of them with Dr. Leidy's type specimen to decide the question. For the present, then, we must recognize six American species of *Xiphactinus*; viz., *X. audax* (Leidy), *X. molossus* (Cope), *X. thau-mas* (Cope), *X. lestrio* (Cope), *X. mudgei* (Cope), and *X. lowii* (Stewart).

In my study of the genus *Xiphactinus* I have been greatly aided by comparison of its various parts with those of the tarpon of our southern coast (*Tarpon atlanticus*). While the tarpon is in many respects quite unlike *Xiphactinus*, in others it strikingly resembles the latter. Although the two genera undoubtedly belong to different families, these families are closely related, and both belong to the order of Isospondyli. It was in this order that Professor Cope arranged *Portheus* and its related genera, but he believed that in them he found also characters which indicated relationship with the Siluroids. Such characters I am unable to perceive. *Xiphactinus* was an Isospondylid, generalized in some respects, but greatly specialized in others. This specialization shows itself especially in the teeth and paired fins.

The head of this genus has been described by Cope (*Cret. Vert.*, pp. 183, 191), by Newton (*Quar. Journ. Geol. Soc.*, vol. xxxiii, p. 505), and by Crook (*Palaontographica*, vol. xxxix, p. 114). Each of these authors also presents figures of various parts. In the following pages I shall call attention to such features of structure as, in my judgment, are new to science, or which require additional treatment or correction.

I regard the identification of the parietals as yet uncertain. Professor Cope was himself in doubt regarding them, and thought that perhaps what he called the supraoccipital might really be the coalesced parietals (*Cret. Vert.*, p. 183). Further

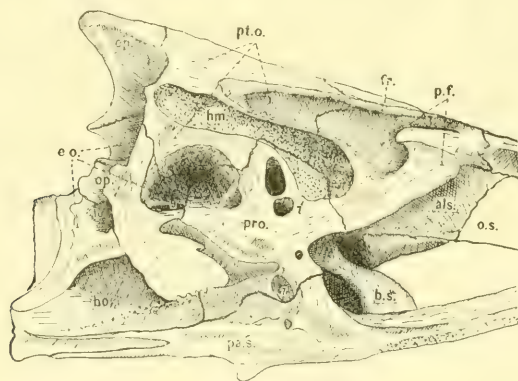


FIG. 1. — Skull of *Tarpon atlanticus*, seen from right side and partly from below.  $\times \frac{1}{2}$ .

on (p. 188) he concluded that the bones which he at first had identified as the epiotics were the parietals. Crook states that the parietals are completely separated by the large supraoccipital: He figures them (Pl. XVIII) as lying laterad of the epiotics, a situation which appears not probable. The small development of the supraoccipital in the tarpon permits the parietals to meet along their whole median borders, while each epiotic (Fig. 1, *cp.*), by its inner anterior angle, comes into contact with the outer posterior angle of the parietal. Should the supraoccipital now be enlarged we might expect the parietals to be reduced posteriorly and more or less separated. It seems to me that in the four rather complete skulls of *Xiphactinus* before me, two belonging to the United States National Museum, the others my own, I can recognize the

parietals as wedge-shaped narrow bones which lie between the anterior ends of the pterotics and posterior ends of the frontals on the outside, and the supraoccipital on the median side. I am inclined to believe that the parietals meet along the mid-line in front of the supraoccipital, and really include the elevated surface assigned by Crook to the latter bone, and said by him to be covered with coarse granulations. The posterior pointed end of each bone falls just mesiad of the epiotic. My determination of these bones may be erroneous, but I am wholly unable to find evidences of any suture defining the parietals as located by Dr. Crook.

The epiotics have been correctly mapped by Dr. Crook. Professor Cope was in doubt about the opisthotics. At first (*Cret. Vert.*, p. 183) he regarded them as forming the postero-lateral angles of the skull; but, on p. 188, he concludes that these angles are formed by the epiotics, and that the opisthotics are absent. Crook (*op. cit.*, p. 115) says that the opisthotics are the largest bones entering into the brain capsule. This I believe to be an error. I am of the opinion that the position and relations of the opisthotics of *Xiphactinus* are best explained by an examination of the tarpon (Fig. 1, *op.*). Here what may be regarded as the body of the opisthotic is rather small. Its upper end articulates with the pterotic (*pt.o.*), while the greater portion of the body lies against the exoccipital (*e.o.*). It bends forward, sending a small process to the proötic (*pro.*). From the lower border of the body of the bone there is sent downward and forward to the basioccipital a broad process which is as large as the remainder of the bone. In passing to the lower portion of the basioccipital, this process forms a bridge across a deep and broad fossa which is excavated in the basioccipital, but the roof of which is formed by the exoccipital. Now, the positions and forms of all the other bones in this region are in *Xiphactinus* almost identical with those of *Tarpon*. There are also the same deep cavities in the side walls of the skulls of the two genera. I believe, therefore, that we are justified in concluding that the opisthotic had somewhat similar form, position, and relationships. Moreover, I am convinced that this bone is present in three of the skulls at my

command ; although, on account of the distortion to which the skulls have been subjected, the determination is not as satisfactory as is desirable. Its lower process appears to have been much slenderer than in Tarpon. In Tarpon the lower process of the post-temporal is attached by a strong ligament to the posterior extremity of the opisthotic ; and, if I am correct in my determination of both these bones in Xiphactinus, they were brought into close connection.

The pterotics (squamosals of most authors) were proportionally more extensive bones in Xiphactinus than in Tarpon, and formed a more prominent process at the outer and hinder portion of the skull. Each included, I am satisfied, the area marked by Crook as belonging to the parietal. The pterotics furnished the larger part of the articular surface for the head of the hyomandibular. This surface was essentially as it is in Tarpon (Fig. 1, *hm.*).

As regards the proötics, Professor Cope's description (*Cret. Vert.*, p. 185) is not far out of the way, though brief. Dr. Crook is less fortunate when he states that the proötics are small. His error arose, if we may judge from his figure of *Ichthyodectes polymicrodus*, from his having carved the opisthotic out of the territory of the proötic. The proötics are really the largest of the otic bones. Professor Cope says that with the pterotic and opisthotic this bone bounded a large foramen. This so-called foramen is not really such, but a deep excavation, or fossa, in the side of the skull. In Tarpon this fossa is an inch deep, and about as much in diameter ; and it was quite as large in Xiphactinus. In the latter genus the anterior wall appears not to have been completely ossified, so that, in the skeleton, the fossa probably opened widely into the large cavity which lay above the brain, and which will be described further on. Since the cavity just referred to was in life probably filled with the primitive cartilage, the apparent opening from the fossa into it was merely an unossified part of the proötic.

In Tarpon the mouth of this fossa is somewhat triangular. Its floor is furnished by the exoccipital and the proötic, its posterior wall by the exoccipital and the pterotic, its roof by the pterotic, and the anterior wall by the pterotic and the



proötic. The sutures between the adjoining edges of each two of these bones meet in the apex of the fossa. The axis of the fossa is directed inward and upward. Without doubt, the fossa in the side wall of the skull of *Xiphactinus* was essentially the same as that in *Tarpon*.

In *Tarpon* there is, as has already been mentioned, an extensive fossa on each side of the skull, excavated principally in the basioccipital. This is so deep that only a thin wall of bone separates that on the right side from that on the left. Each fossa is continued forward on the outer surface of the proötic, becoming narrower and shallower. It is across this fossa that the broad process of the opisthotic is thrown as a bridge. A somewhat similar fossa existed in *Xiphactinus*, but on account of the compression suffered by the skulls its features cannot be definitely determined.

The proötic of *Xiphactinus*, like that of *Tarpon* (Fig. 1, *pro.*), provides a portion of the articular surface for the head of the hyomandibular. In *Tarpon* there are on the external surface of the proötic some four or five foramina. In *Xiphactinus* I have been able to detect only one of these, that for probably a branch of the facial nerve. It lies just below the anterior end of the articulation of the hyomandibular, and corresponds to that marked  $\gamma'$  in the figure of *Tarpon*. In *Tarpon* this foramen opens into a canal which runs backward in the proötic and emerges at the hinder border of the mouth of the fossa, above described as being walled in by the proötic, opisthotic, and exoccipital. This canal is then continued backward on the outer surface of the exoccipital beneath the opisthotic. It — or, at least, its hinder portion — serves to conduct the glossopharyngeal nerve. An opening has been found in *Xiphactinus* in the mouth of the fossa, and doubtless the canal was similarly prolonged both forward and backward.

Crook's statement that the parasphenoid is triangular in section, with the base of the triangle directed upward, is true only when the skull is held in an inverted position. The error is doubtless due to a slip of the pen. It is also erroneous to say that the finger-shaped processes outstanding from each side of the parasphenoid arise at the union of the parasphenoid and

basioccipital. They arise about opposite the union of the basisphenoid and the parasphenoid. These strong lateral processes are almost wholly absent in Tarpon. In both this genus (Fig. 1, *pa.s.*) and Xiphactinus there is, on each side, a strong process arising from the parasphenoid to meet the proötic. These processes form the side walls of the muscular canal. This canal was of greater extent perpendicularly in Xiphactinus than in Tarpon.

The basisphenoid is a Y-shaped bone, the upper end of which articulates with the proötics, while the lower end rests on the parasphenoid. It is almost twice as long as the corresponding bone in a tarpon of the same size (Fig. 1, *b.s.*).

So far as can be determined from the crushed skulls of Xiphactinus, the form and relationships of the alisphenoids and the orbitosphenoids were very much the same as in Tarpon. In this latter fish both of these pairs of bones are large (Fig. 1, *als., o.s.*). The alisphenoids meet in the mid-line, below the brain, and thus continue forward the floor of the brain-case. In front of these are the large orbitosphenoids, ankylosed in the mid-line, as in the salmon. There is no distinct presphenoid.

In the tarpon the brain-case is roofed over behind by the supraoccipital. In front of this the proötic sends upward and inward a plate of bone which meets a similar plate from the opposite proötic. This roof is continued forward by plates of bone which grow mesiad from both the alisphenoids and the orbitosphenoids. These two pairs of bones also send out great lateral plates, which abut against the postfrontal and the lower surface of the frontal. In the mid-line above the brain, the united orbitosphenoids send upward a more or less interrupted crest of bone. Between the brain-case, as thus roofed over, and the parietals, pterotic, and frontals, there is a great space an inch high and extending from one side of the skull to the other, and in life this is probably filled with the primitive cartilage. The arrangement of this portion of the head may be understood by an examination of Parker's figures of the salmon (*Trans. Phil. Soc. London*, vol. clxiii, pp. 95-145, Pls. I-VIII). In Tarpon there are two foramina in the proötic which open from the outside into the cavity here described. One of these is

found in the lower anterior angle of the great lateral fossa; the other is seen just above the foramen 7'. These foramina are probably closed with membrane in life. They are not found in *Xiphactinus*.

In *Xiphactinus* the alisphenoids and the orbitosphenoids appear to have had the same extent and relations, at least as seen from below, and I have no doubt that there was in the skull the same large amount of primitive cartilage that we find in Tarpon to-day.

The frontals of *Xiphactinus* were much broader than they are in Tarpon. In a tarpon whose skull had to one of *Xiphactinus* the ratio in length of 9.5 to 10.5, the width of the frontals bore the ratio of 1 to 2. Since the breadth of the nasal region of *Xiphactinus* was little less, we may appreciate Professor Cope's characterization of their expression as being bulldog-like.

To a broad flat surface of the very stout prefrontal of *Xiphactinus* was applied the superior articulating surface of the malleolar body of the palatine. In Tarpon the palatine is similarly connected with the prefrontal, except that the ethmoid bone sends outward a process which takes part in the articulation. Professor Cope states that in the alewife the articulation of the palatine is wholly with the ethmoid.

The lower surface of the ethmoid furnishes an articular surface for the anterior condyle of the maxillary. Since this condyle in *X. thauomas* is much larger than that of *X. molossus*, we ought to find a corresponding difference in the ethmoids of the two species.

There can be no doubt that the orbit of *Xiphactinus* was surrounded by a ring of orbital bones, just as it is in Tarpon. In a skull of *X. molossus* before me (No. 1646, U. S. N. M.), the superorbitals are wanting, but the border of the frontals shows distinctly that a row of thick bones has been articulated with it. In Tarpon there are three of these superorbitals. Crook has figured a preorbital in *Xiphactinus*.

In Tarpon the posterior suborbitals are very large, extending backward over the cheek as far as the preopercle. In nearly their whole extent they are membranous. It is certain that

they were quite as extensive in *Xiphactinus*, and composed of very thin bone. Crook has figured them as extending well back from the orbit, and I find them pressed down on the metapterygoid and hyomandibular of *X. thaumas*.

Dr. Crook states that the ossified sclerotic of *Xiphactinus* forms a complete ring, meaning, I take it, that it does not consist of more than one piece of bone. Having a portion of the sclerotic in my possession which closely resembles those figured by Professor Cope (*Cret. Vert.*, Pl. XL, Fig. 3; Pl. XLIII, Fig. 4), I am inclined to believe that the sclerotic consisted of two separate pieces of bone, and this is the usual condition of the sclerotic of fishes.

No one has yet, so far as I know, described the nasals, and I have not succeeded in identifying them. In Tarpon each of these bones is a rugose scale which lies partly on the outer border of the ethmoid. It might easily become detached during maceration, and this accident may have happened to this bone in the skulls of *Xiphactinus* that I have examined.



FIG. 2. — *Xiphactinus thaumas*, maxillary and premaxillary, seen from above.  $\times \frac{1}{2}$ .

The maxillaries and the premaxillaries are the most characteristic bones of this genus, and especially on the number and the character of the teeth borne by them have been founded most of the different species. Frequently, however, the premaxillary has been separated from the maxillary. I believe that the species may be identified from the condyles of the maxillary. At least, these condyles are quite different in the two species which I have been able to examine, *X. thaumas* and *X. molossus*. Fig. 2 represents the maxillary of the former species, Fig. 3 that of *X. molossus*. From these figures it will be seen that in *X. thaumas* the posterior condyle (*p.mx.c.*) is notched behind, while that of *P. molossus* is excavated in front.

It appears, too, that the condyle is more extended longitudinally in *X. thaumas*, more transversely in *X. molossus*. Examining the anterior condyle, the one which



articulates with the ethmoid, we find that in *X. thaumas* it is large and elongated, and approaches the posterior condyle within a distance equal to half its own length. In *X. molossus* the condyle is much smaller, regularly oval, and far removed from the posterior condyle. It is to be expected that the other species of the genus will exhibit likewise their distinctive characters. I am inclined to believe that these condyles underwent some individual variation, and they have in many cases suffered distortion during fossilization, and this must be taken into account. The left maxilla belonging to the same individual of *X. molossus* from which Fig. 3 was drawn possessed an additional condylar surface, nearly round and small, just in front of the posterior condyle. It is to be inferred that the ethmoids of the various species, and especially the surface of the palatine with which the posterior maxillary condyle articulates, will exhibit characters corresponding to those shown by the latter.

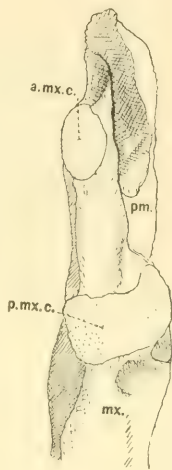


FIG. 3. — *X. molossus*, maxillary and premaxillary, seen from above.  $\times \frac{1}{2}$ .

I call attention to the fact that it is as yet difficult to distinguish the various species by means of characters furnished by the lower jaws. In the case of *X. molossus* there are discrepancies between Professor Cope's description of the number and character of the teeth and one of his figures. The lower jaw of the type specimen is figured on Pl. XXXIX of the *Cretaceous Vertebrates* and again on Pl. XL, Fig. 1. The statement is made in the text (p. 195) that there are in all 20 teeth; but in the figure last referred to there are 27 teeth represented, and these do not all agree in size either with the statements of the text or with the other figure. The explanation of this discrepancy, evidently, is that the figure on Pl. XL has, so far as many of the teeth are concerned, been erroneously restored. *X. thaumas* is said (*op. cit.*, p. 197) to have rather more numerous teeth than *X. molossus*, and in the specimen described there are said to be 23. I possess two dentaries which I regard as belonging to *X. thaumas*. In these there are 24

teeth, and their sizes and arrangement agree well with Cope's figure of the dentary of this species presented by him (*Cret. Vert.*, Pl. XLIII, Fig. 3). Probably it will be well not to rely too much on the number of the teeth as a specific character.

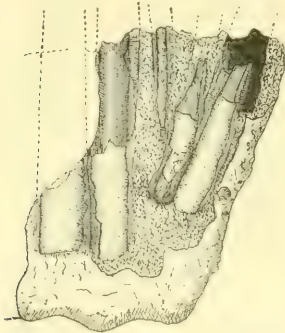


FIG. 4.—*Xiphactinus*. The mandible near symphysis, with bone broken away to show the roots of the teeth.  $\times \frac{1}{2}$ .

Professor Cope states (*Proc. Amer. Philos. Soc.*, vol. xii, p. 175) that the teeth of these fishes descend in their alveoli to the depth of an inch. The large teeth really have much longer roots than thus indicated. In the lower jaw the bases of the large teeth near the symphysis descend nearly to the lower border of the jaw. Fig. 4 presents a view one-half the natural size of the symphyseal end of the mandible of a species of *Xiphactinus*, seen from the outside. The bone has been broken away so as to expose the roots of the teeth, and portions, too, of these are missing. The teeth in life had a very large pulp, and the cavity containing this pulp had, since burial, been filled up with crystallized calcite. This, in the drawing, is stippled. Where the calcite has fallen out and exposed the inner surface of the dentine the shading has been made by perpendicular lines. The broken edges of the dentine itself are shaded by horizontal lines.

Cope and Crook have both figured the articulation of the lower jaw with the quadrate. It appears to me that the figures of both are more or less erroneous, or, at least, misleading. Professor Cope (*Cret. Vert.*, p. 194) states that the articular is distinct, wedge-shaped, short, and supports half the cotylus. He describes the angular as having a prominent angle, like half an ellipse, and extending in a long sword-shaped process

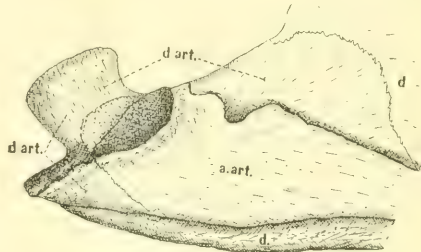


FIG. 5.—*Xiphactinus*. Proximal end of lower jaw.  $\times \frac{1}{2}$ .

on the inside of the ramus to beyond its middle. A lower jaw of *Xiphactinus* (No. 3782, U. S. N. M.), in almost perfect condition (Fig. 5), enables me to correct some of these statements. Cope's articular is not short, but its continuation forward forms the long sword-shaped process that he regards as belonging to the "angular." In short, this articular corresponds to the autarticulare of Van Wijhe (*Niederländ. Archiv. f. Zool.*, vol. v, pp. 207-320) and originates from the ossification of Meckel's cartilage. Cope's angular is not the true angular, but is Van Wijhe's dermarticulare, a membrane bone. In *Lepisosteus*, *Amia*, and *Polypterus* these bones remain distinct. Van Wijhe (*op. cit.*, pp. 306, 307) makes the following statement in speaking of the elements of the lower jaw of the genera mentioned above: "Eine Vergleichung mit den Teleostiern zeigt, dass was bei diesen als Articulare angegeben wird durch eine Verschmelzung des Autarticulare mit dem Dermarticulare entstanden ist." Here, however, in this Cretaceous genus of Teleosts, we find these elements still distinct from each other. In the genera of so-called Ganioids referred to above the autarticulare is very short; but, relying on two good specimens of *Xiphactinus* and one of *Ichthyodectes*, I am confident that the proximal end of the autarticulare is continuous with the long sword-shaped process described by Cope, and that this process is entirely distinct from the dermarticulare.

If the true angular ever was present in *Xiphactinus*, it has become consolidated with the dermarticulare. In a specimen of *Ichthyodectes* there is present a surface to which an angular seems to have been sutured. Crook represents it as present.

Professor Cope's figure of the lower jaw of *Xiphactinus* (*Cret. Vert.*, Pl. XXXIX) at first sight gives one the impression that the rounded head of the quadrate articulated with a similar rounded head belonging to the lower jaw. The latter, however, is the "prominent angle, like half of an ellipse," and the quadrate was supposed to enter its cotylus mesiad of this angle and well forward. My Fig. 5 shows the jaw seen from within. The cotylus is furnished partly by the autarticulare and partly by the dermarticulare. The head of the quadrate sits in its cotylus on the mesial side of the broad process of

the dermarticulare. I know of no recent fish which possesses such an arrangement. The tarpon has a very different articulation in this region, since it resembles closely the articulation between two vertebrae of a bird. The advantages of such an articulation as that of *Xiphactinus* are obvious, since this species doubtless preyed on large fishes, and possibly on some of the large aquatic reptiles of its era. Fig. 6 represents another specimen of the jaw of *Xiphactinus* (No. 1646, U. S. N. M.). At *q.c.* is seen the condyle of the quadrate; *ep.h.* is the lower end of the epihyal, and *c.h.* the upper end of the

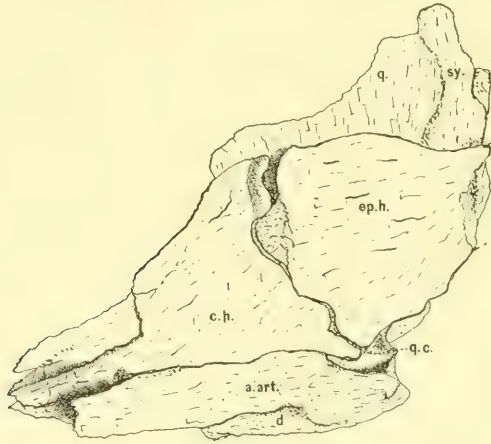


FIG. 6. — *X. molossus*, showing quadrate, autarticulare, and hyoid bones.  $\times \frac{1}{2}$ .

ceratohyal. These bones are closely appressed to the inner surface of the quadrate and of the lower jaw.

The entopterygoid, or mesopterygoid (Fig. 7, *m.pg.*), has a smooth, slightly convex surface sloping inward and upward to form a partial floor for the orbit. Unless its width has been excessively altered by pressure, it was much narrower than the corresponding surface of Tarpon. In the latter the entopterygoid meets the upper anterior angle of the quadrate, these two bones thus excluding the ectopterygoid from contact with the metapterygoid. In *Xiphactinus*, on the contrary, these two last-mentioned bones have a considerable union (Fig. 7).

The bones of the palato-quadrate arch have been described as being devoid of teeth. I have, however, found a consider-



able patch of small teeth on the entopterygoid (Fig. 7, *t.*), and another smaller patch on the ectopterygoid (Fig. 7, *t.*<sup>1</sup>). In the Tarpon teeth occur on the vomer, parasphenoid, pterygoids, and even on the quadrate.

The hyomandibular (Fig. 7, *hm.*) is in many respects like that of Tarpon, but, like the other bones of the extinct genus, is of more massive construction. The anterior border of the

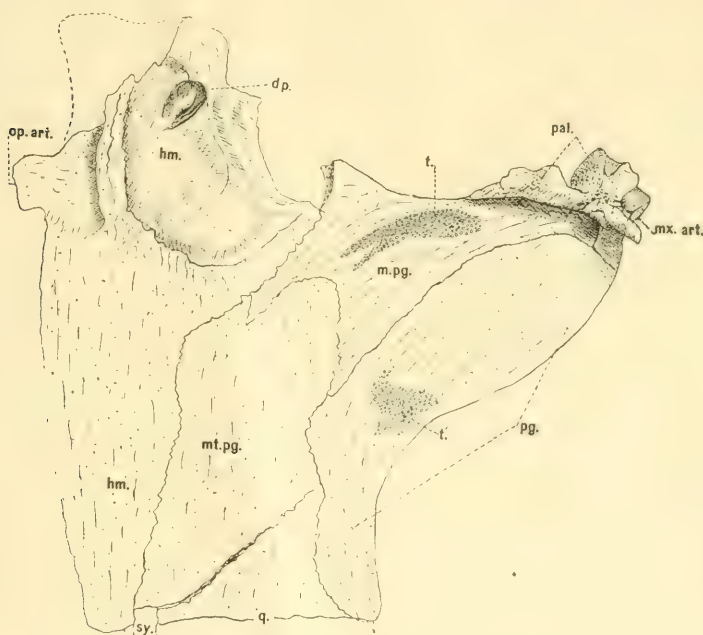


FIG. 7. — *X. thaumas*. Hyomandibular and palato-ptyergoid bones.  $\times \frac{1}{4}$ .

bone extends further forward than it does in Tarpon. In the latter the anterior border falls, with a sigmoid curve, in a general downward direction, crossing the posterior angle of the metapterygoid. In Xiphactinus the anterior border of the hyomandibular runs rapidly forward, so as to come into contact with and pass mesiad of the posterior border of the entopterygoid. The greatest width of the hyomandibular from the articulation of the operculum to the anterior border is nearly equal to the distance from the anterior border to the anterior end of the palatine. In Tarpon the latter distance is about 2.5 times the greatest width of the hyomandibular. However,

on account of the relatively greater depth of the head in *Xiphactinus*, the width of its hyomandibular has about the same ratio to its length that we find in Tarpon.

In Tarpon the process for articulation of the operculum projects from the hinder border of the bone more than in *Xiphactinus*. In the latter genus the surface for the operculum of *X. molossus* scarcely passes beyond the border of the bone; but in *X. thaumas* the surface is at the extremity of a considerable process.

As a result, perhaps, of its large size, the hyomandibular of *Xiphactinus*, as well as that of Tarpon, is provided with prominent ridges and depressions, and with foramina leading into its interior. Many of these are repeated in the two genera with much faithfulness. In both genera there is found running down near the middle of the outer surface of the bone a high crest, like the spine of the human scapula. This crest has its origin, we may say, in two low rounded ridges, one beginning at the anterior end of the hyomandibular head, the other at its posterior end, the two ridges converging and meeting opposite the articular surface for the opercular. Here the resultant crest becomes much more elevated, thin, and sharp, and continues to the lower end of the bone. The plane of the crest is directly outward and slightly backward. Both in front and behind the crest is a deep fossa, the posterior one the best defined. The anterior border of the preopercular occupies a part of the posterior fossa. This fossa, in Tarpon, ends above in a deep depression immediately in front of this process for articulation of the opercular; but from the upper border of this depression one or more large canals enter the bone, and, passing upward, emerge by several mouths in another depression on the inside of the bone just below the head of the hyomandibular. It is quite probable that one or more branches of the facial nerve pass downward through these canals.

In *Xiphactinus* the posterior fossa ends above, just as described, and broad channels are seen passing upward from it in the bone; while on the outside, just below the anterior end of this hyomandibular articulating surface, there is a depression

like that found in Tarpon. There can be no doubt, therefore, that the upper end of this hyomandibular is hollowed out similarly in the two genera. In a specimen of *X. molossus* before me, two bridges of bone are thrown across the upper end of the posterior fossa on the mesial surface of the hyomandibular. On the same surface of the hyomandibular there is a well-marked median crest, in front of which is a broad shallow fossa. It is in the upper end of this fossa that the depression is found that has just been described, and which in *Xiphactinus* is represented in Fig. 7, *dφ*. This depression, it is to be noted, faces the deep fossa which has already been described as occurring in the side wall of the skull. Its significance can only be determined by an examination of a fresh Tarpon. Both depressions probably furnish insertions for muscles.

The opercular of this genus is not well known. Cope states that it is thin and broad. Crook figures a portion of the bone, but this reaches downward only about to the middle of the preoperculum. I have a fragment of a bone 50 mm. by 100 mm. which appears to be the opercular of *X. thaumas*, and this, too, has every appearance of ending about halfway down the preoperculum. This piece of bone has an articular surface resembling that of Tarpon for connection with the preopercular, and, like Tarpon, there are just below this surface, and on the inner side of this bone, one or two large openings into the interior of the bone. This mention of the opercular may attract attention to it. It appears rather improbable that it is really so short as above described.

In each of the three specimens of *Xiphactinus* before me there is present, attached to the posterior outer angle of the skull, a bone which seems to occupy the position of the post-temporal. If such it is, it was very different from that of Tarpon. It is not much over an inch in length, and less than two inches broad, but very thick. In a specimen of Tarpon the bone is rather thin and much longer. In *Xiphactinus*, on account of the crushed condition of the skulls, the relations of the bone are hard to make out, but it seems to be connected with the opisthotic and the epiotic. In many fishes the post-temporal bone is very short and stout.



If I have correctly determined the bone figured here (Fig. 8), the supraclavicular, by its great length, compensated for the shortness of the post-temporal. Its length is about equal to that of the parasphenoid.

The shoulder girdle has received very unfortunate treatment. It appears to have been misunderstood by both Professor Cope

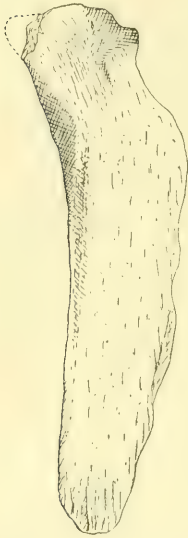


FIG. 8. — *X. molossus*.  
Suprascapula?  $\times \frac{1}{2}$ .

and Dr. Crook, being by both writers described in an inverted position. Cope gives figures in his *Cretaceous Vertebrates* as follows: Pl. XL, Fig. 9 (cleithrum?); Pl. XLII, Figs. 2-5; Pl. XLIV, Figs. 10, 11. Most of these depict the scapula and the parts immediately adjacent. Cope describes the "coracoid" as a stout flat rod, narrower than the cleithrum (clavicle), and appressed to the inner face of the latter nearly to its distal end (*Cret. Vert.*, p. 186). He was unable to state whether or not there was present a precoracoid, but said that the "coracoid" occupied the position of the precoracoid in some fishes. According to his conception, the scapula was placed high up on the body, although his restoration of the fish on Pl. LV does not so indicate. Dr. Crook

has presented figures of the girdle of *Xiphactinus* (*op. cit.*, Pl. XVII), of his *Ichthyodectes polymicrodus* (Pl. XVI) and of *I. anaides* (Pl. XV). There can be no doubt that all these figures represent bones which belong to the side of the body opposite to that to which they are assigned, and that what is regarded as the ventral end is the dorsal. To demonstrate this it is only necessary to compare the figures with the prepared shoulder girdle of a shad. Dr. Crook recognized that Professor Cope's coracoid was really the precoracoid; nevertheless, he has represented it as running ventrally from the coracoid, instead of toward the dorsal end of the cleithrum.

One result of Crook's error is that the coracoid is brought into a position dorsad of the scapula. The materials employed by both Cope and Crook were defective, that portion of the



cleithrum and coracoid belonging ventrad of the fin articulation being mostly wanting. Fortunately I have on one block both the right and left halves of the shoulder girdle in nearly perfect condition. To one half are also attached some of the remarkable fin rays of this genus. A figure is presented of the right half of the girdle seen from without (Fig. 9). In this figure the cleithrum conceals a part of the coracoid,<sup>1</sup> but the latter is so broad that a considerable portion of it is seen. In *Tarpon* there is along the upper border of the coracoid a long fontanelle between this bone and the cleithrum. If such a fontanelle was present in *Xiphactinus* it is concealed beneath the cleithrum. In *Tarpon* there are two or three foramina in the coracoid just below the scapula. They are in

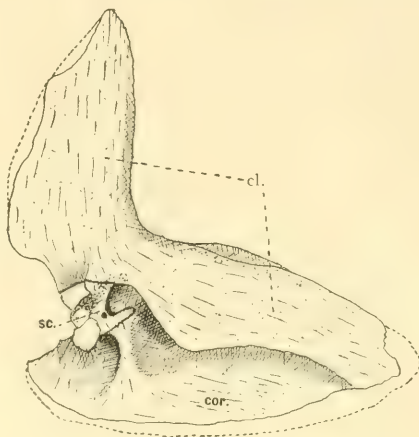


FIG. 9. — *Xiphactinus*. Shoulder girdle.  $\times \frac{1}{4}$ .

life closed by membrane. They are wanting in *Xiphactinus*. The outer surface of the dorsal limb of the cleithrum of *Xiphactinus* is broad and convex to the very hinder border. It thus resembles *Tarpon*, and differs from *Alosa sapidissima*, in which the hinder portion of this surface is rough and excavated for muscles. In the extinct genus there is an extensive fossa on the inner surface of the upper limb of the cleithrum. The upper half of this fossa lies between an outer and an inner plate of the cleithrum. Further down, the fossa is limited mesially by the precoracoid. There seems to be no such fossa in *Tarpon*, and that of *Alosa* is very shallow. In both *Tarpon* and *Alosa* the precoracoid is a much less important bone than it is in *Xiphactinus*.

<sup>1</sup> I employ for the elements of the shoulder girdle the terms in common use, except that I use Gegenbaur's name cleithrum instead of clavicle. For the latter element Dr. Gill has proposed the term proscapula; for coracoid, hypocoracoid; for scapula, hypercoracoid; and for precoracoid, mesocoracoid.

The pectoral fins have been described by Professor Cope and Dr. Crook (Cope, *Cret. Vert.*, pp. 186, 193, 204; Crook, *Palaeontographica*, vol. xxxix, p. 119). Neither of these authors compares the fin structure with that of other fishes, although a community of structure is perhaps implied. The large saber-shaped spines, each consisting of an upper and a lower half, are remarkable enough; but when comparison is made with the fins of a shad or of a tarpon the arrangement of all the parts is easily comprehended. The first pectoral ray of *Xiphactinus* resembles quite closely that of Tarpon. It differed in being, relatively to the size of its owner, somewhat, but not enormously, larger. It differed further in having lost, apparently to the very tip of the ray, the cross-segmentation. In Tarpon this persists in the distal half of the ray. Doubtless, the spine-like rays of *Xiphactinus* were not so flat as they are now presented to us. It is quite probable that the rays succeeding the first one were,

toward their distal extremities, not only cross-segmented, but also longitudinally split, as in other fishes.

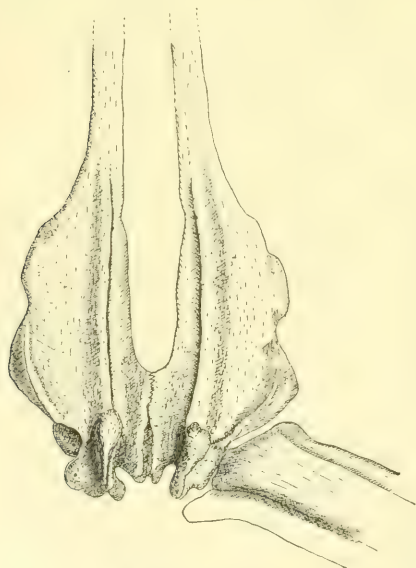
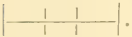


FIG. 10. — *X. thauomas*. Pelvic bones and base of fin.  $\times \frac{1}{4}$ .

Professor Cope (*Cret. Vert.*, p. 186) has described the ventral fins and their supporting bones. The latter, pelvic actinosts, usually termed the pelvic bones, are called by Professor Cope the femora. He also figures them (p. 192, Fig. 9, and Pl. XLV, Figs. 7, 7a). I possess a well-preserved specimen of the pelvis and the ventral fins of *X. thauomas*, and from these it becomes evident

that the pelvis figured by Professor Cope was very defective. This may be seen by comparing the figures above referred to with my Fig. 10, which represents the pelvic actinosts seen

from below. These pelvic bones are, as stated by Professor Cope, massive, and expanded vertically on the outer side to support the facets for the ventral fin.

The right and left bones are strongly sutured together. In front of the facets and of the suture the bones become much thinner, but wider. At the same time there is, descending from the outer border of each bone, a crest of moderate height, while from the same portion of the outer border there arises a much higher crest, so that a cross-section of the pelvis in front of the fin articulation would somewhat resemble this figure . Just laterad of the inner border of each bone there is found on the upper side a prominent ridge, running from the fin articulation toward the anterior end of the bone. On the lower side, and nearly opposite the upper ridge, is a similar ridge. Elsewhere the bone is very thin. If now the thin portions of bone were broken and had crumbled away, there would be left a thick process standing out on each side and two rods, the ridges just described. Such was doubtless the condition of the bones which Professor Cope figured. Just how far forward the pelvic actinosts extended is not known, since those figured by both Professor Cope and myself have been broken. In Tarpon these bones are very long and slender. In Elops, a close ally of Tarpon, they are relatively shorter and also broader behind.

Professor Cope has quite correctly described the facets for articulation of the ventral fin. My Fig. 11 represents the positions and forms of these facets. The bone is that of the right side, and is looked at laterally. The upper facet is for the reception of an articular surface on the base of the upper half of the first ventral ray; the large lower facet for an articular surface on the lower half of the same ray. The other two facets are for succeeding rays, or possibly for baseosts. There was undoubtedly a disc-like baseost between the upper half of the first ray and the articular surface of the pelvic bone; and there may have been other rudimentary baseosts.

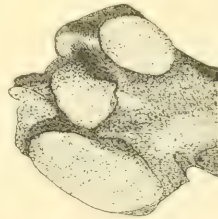


FIG. 11. — *X. thauwas*. Side view of articulation for pelvic fin.  $\times \frac{1}{2}$ .

The planes of the two surfaces which support the first ray approximately coincide and are directed outward, somewhat backward, and slightly downward, a position different from that given by Cope.

The first and spine-like ventral ray is constructed like the first pectoral, and may also be compared with that of other *Iso-spondyli* such as the lake-trout (*Cristivomer*) and tarpon. Like the first pectoral ray, it seems to have wholly lost its transverse segmentation. These spines, however, show no special physoclistous characters, as Professor Cope supposed they did. The first ray of my specimen of the ventral fin of *X. thaumas* is 38 mm. wide at the base, and was perhaps originally 60 cm. long; but this was a very large fish, since its upper jaw had a length of 38 cm. Professor Cope states that the first three rays were spines, and that there were probably no additional rays. However, it seems probable that the rays succeeding the first one were much feebler, were segmented, and longitudinally split. There were certainly more than three rays, for, in my specimen, I make out six or eight, and there were probably nine. The second ray has only about one-third the diameter of the first, and those following become gradually, probably rapidly, reduced. The inner rays must have been very short, since I find finely split and segmented rays at a distance of only 90 mm. from the base of the rays. In Fig. 10 I have represented the bases of the first and second rays. On the anterior border of the first ray the broader upper half of the ray is seen to project some distance beyond the lower half. It will be noticed, also, that on account of the expansion of the pelvic bone in front of the fin articulation, the fin could not be brought in front of a perpendicular to the body at that point.

In *Cristivomer* and *Tarpon* I find a rudimentary ray in front of, and lying on the base of the first ray. It is short, but has a very long muscular process directed forward and upward. It is more reduced in *Tarpon* than in *Cristivomer*. I find no evidence of its presence in *Xiphactinus*.

The vertebral column has been described by Professor Cope (*Cret. Vert.*, pp. 188, 193, 195, 199), and briefly by Dr. Crook (*op. cit.*, p. 117). I have noted some hitherto undescribed



peculiarities which are of interest. I have a considerable number of the vertebrae of *X. thaumas*, including unconnected vertebrae belonging to the anterior portion of the column, and a section about two feet in length from the tail region. I have also numerous vertebrae belonging to some indeterminable species, probably *X. molossus*. Access is permitted me to vertebrae of probably *X. molossus*, belonging to the United States National Museum. These belong mostly to the tail. I will first describe the peculiar structure of the neural arches in the latter region. The drawing presented will assist in the understanding of my description (Fig. 12). The neural arches here, as elsewhere in this fish, are connected with the centra

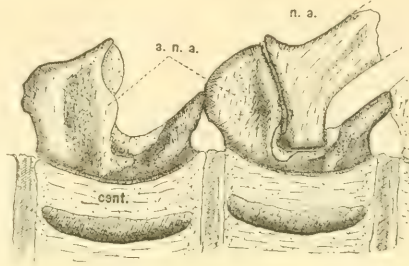


FIG. 12. — *X. thaumas*. Two tail vertebrae.  $\times \frac{1}{4}$ .

by suture, and have usually fallen out before burial, leaving long grooves where their bases were inserted. This was the case with the third vertebra behind the right-hand one shown in Fig. 12. When we come to examine the arches more closely we discover that each lateral half is not a single piece, but consists of two pieces, a basal piece (*a. n. a.*) and the arch proper (*n. a.*). That the proper arch is a distinct piece is shown, not only by the existence of a suture, but likewise by the fact that in the vertebra on the left hand of the figure the arch has fallen out of its place before fossilization. The basal or accessory piece is inserted by a shallow gomphosis into the centrum for nearly the whole length of the latter. It rises high in front and projects so far forward as to come into contact with the basal piece of the next vertebra in front. Behind, the basal piece is directed upward and backward in a rather slender process, which abuts against the anterior edge of the basal piece of the next vertebra behind. It is thus seen that these basal pieces provide the anterior and posterior zygapophyses. They remind us of the articulating processes of certain other fishes, Mugil, etc. Between the anterior and posterior

processes the basal pieces are excavated to receive the bases of the neural arch, as shown in the figure. The two basal pieces of each vertebra are distinct. Together they seem to form a saddle in which rides the neural arch.

I find this same structure of the neural arches in some of the vertebrae belonging to the specimens in the United States National Museum; but in one section of connected vertebrae an arch like those above described is succeeded in the next vertebra behind by an arch in which every trace of a suture between the arch and the apparent basal piece is lost. This vertebra is shown in Fig. 13. The form of the base of the arch is not greatly different from that of the arch with accessory piece in Fig. 11, and we may even convince ourselves that we can trace a part of the boundary line between the two portions. There is evidently at this point of the vertebral column a sudden change from neural arches furnished with basal accessory pieces to arches without these, or consolidated with them. Further backward the form of the arches becomes modified somewhat, so that they resemble the one shown in Fig. 14. A section 14 inches



FIG. 13.—Xiphactinus. Transitional neural arch.  $\times \frac{1}{4}$ .



FIG. 14.—Xiphactinus. Neural arch without accessory piece.  $\times \frac{1}{4}$ .

long and containing 7 vertebrae having arches of this kind is before me. This condition shows us that the neural arches which are provided with basal pieces are confined to the anterior or middle portion of the tail region, while the hinder portion contains no such vertebral structures. We are reminded that in *Amia* the middle portion of the caudal vertebral column is composed of two rings for each muscular segment, while the anterior and posterior portions have vertebral centra of the ordinary kind. It seems as if the tail portion of the vertebral column of the Amioid fishes and of the Isospondyli retained primitive conditions longer than the abdominal portion.

It is difficult to determine what explanation is to be given of the presence of these basal pieces.

The so-called zygapophyses of fishes are regarded as being outgrowths from the neural arches, exogenous and not autoge-

nous processes. It might be said, possibly, that the basal pieces are the proper arches, while the pieces which are borne on them are the spinous processes. I hold that there are two objections to this view. The first is, that what are sometimes called free spinous processes are always unpaired pieces. The second is, that when the lateral halves of the arches remain distinct from each other and are prolonged into spines, as they are in various fishes, *Amia* and *Salmo*, for instance, the spinous portion is never, so far as we know, developed in the embryo as pieces separate from the base of the arcuale. This is true in the case of *Amia*, which I have investigated. We must, therefore, seek some other explanation. The key to the understanding of the problem is, it seems to me, to be found in the vertebral column of that primitive fish, *Amia*. We may call this fish to our assistance since the *Isospondyli* are believed to have had ancestors not far removed from *Amia*.

In the middle region of the tail of *Amia* there are for each muscular segment two vertebral rings, the one bearing the arches, upper and lower, the other archless. If a transverse section be taken through the middle of the arch-bearing ring, there will be found an X of cartilage, the upper arms of which are continuous with the cartilage of the neural arch. In like manner the lower arms will be seen to be continuous with the cartilage of the haemal arch. If a section is made similarly through the archless disc, a similar X of cartilage is found; but the arms project beyond the outer surface of the disc but a short distance. These archless discs are developed in *Amia* from ossifications arising in the intercalated cartilages, upper and lower, and the arms of the X are the unossified portions of these cartilages. There appears to be no reason why these intercalated cartilages should not sometimes take on a hypertrophied growth. In the sharks they often become considerably larger than the true neural arches themselves.

In case these intercalated cartilages should become thus enlarged and arch-like, each might develop a bony investment that would simulate the bony neural half-arch, and thus would rest on the top of its proper epicentrum.<sup>1</sup>

<sup>1</sup> For figures illustrating the architecture of the vertebral column of *Amia*, see the May number of the *American Naturalist* of the present year.

Coming now to the anterior region of the vertebral column of *Amia*, we find that each vertebra is formed through the suppression of certain of the elements which, in the tail region, constitute the vertebral rings or discs, and the union of the remaining elements of each muscular segment into a single mass. The lower intercalated cartilages are suppressed. The upper intercalated cartilages hypertrophy, and their ossifications unite with the bones developed in the bases of the lower arch, thus giving origin to the centrum. The ossification that we might expect to find developing in the base of the cartilaginous neural arch, the epicentrum, is aborted, while the ossification of the enlarged intercalated cartilage, the pleurocentrum, pushes itself into the place of the epicentrum, and thereafter supports the neural arch.

Now we have the choice of two suppositions, neither of which, however, may be the true one. We may hold that a distinct bone was developed in the somewhat elongated and projecting intercalated cartilage, and this, of course, rested on the top of the pleurocentrum; when the latter was pushed forward beneath the neural arch to take the place of the aborted epicentrum, this newly developed bone was carried along and was thus brought between the pleurocentrum and the base of the neural arch.

Or we may hold that the bone which I have found in *Xiphactinus* supporting the true neural arch is simply the epicentrum itself, aborted, indeed, in *Amia*, nevertheless persisting in *Xiphactinus*, but crowded upward out of its original seat on the notochord.

Either of the above suppositions presupposes that the upper half of the vertebral centrum takes its origin from the pleurocentrum. Professor Cope held that the vertebrae of fishes are "intercentra," that is, have originated in the suppression of all the other elements through the excessive development of the hypocentra. But the very existence, in many genera, of a cartilaginous X in a transverse section of the centrum is proof that its upper portion has been derived from either the bases of the upper arches or the pleurocentra. The deep gashes in the vertebral centra of *Xiphactinus*, where the arches have



fallen out, furnish evidences that this cartilaginous X was present.

The anterior neural arches of *Xiphactinus*, probably all of those belonging to the abdominal region, are very different from those of the tail. One of these abdominal neural half-arches, as seen from without, is presented in Fig. 15; another, seen from the mesial side, is given in Fig. 16. These neural arches are coössified neither with the vertebral centra nor with their fellow bones. The base is hemispherical and planted in a broad excavation in the upper surface of the centrum. The two excavations of each centrum are close together, and it seems probable that the juxtaposed borders of the right and

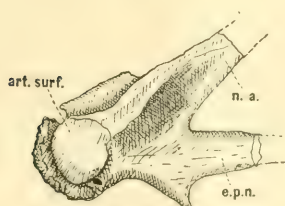


FIG. 15.

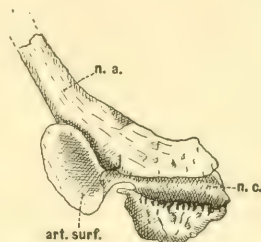


FIG. 16.

FIG. 15. — *X. thaumas*. Neural arch near head, seen from without.  $\times \frac{1}{2}$ .

FIG. 16. — *X. thaumas*. Neural arch near head, seen from within.  $\times \frac{1}{2}$ .

left elements of each arch are in contact both below and above the neural canal. Behind the base of the neural half-arch is a broad smooth surface (Fig. 16, *art. surf.*) looking mesially, and in life coming into contact with a similar surface on the anterior end of the next vertebra behind and looking outward (Fig. 15, *art. surf.*). These surfaces remind us strongly of the zygapophyses of the higher animals.

At the base of each of these half-arches we find a strong rod-like process directed outward and backward. These processes are the epineurals (Fig. 15, *e.p.n.*). They were confluent with the bases of the arches just as they are in *Alosa* and *Tarpon*. It is entirely probable that *Xiphactinus* and its allies were as bony fishes as our just-mentioned modern genera.

The excavations for the insertion of the neural arches are broadest toward the region of the head. Farther backward

they become longer and narrower. Professor Cope describes all the centra as having on each side two lateral grooves, except the two or three centra near the head, called by him the "cervicals." However, so far as I can determine, the vertebral centra of the abdominal region have only one lateral groove on each side. Close to the head this groove becomes quite insignificant and is placed close to the pit for the neural arch.

The attachment of the ribs deserves notice. They are not joined directly to the centra but through the medium of distinct pieces of bone, the parapophyses. These are very short, and are sunken in circular pits so deeply that they scarcely rise above the surface of the centrum. Each has a concavity for the reception of the head of a rib. Some specimens in my possession have the parapophysial pits empty. In others the parapophyses are present, but without rib heads. In a few the head of the rib yet remains.

Distinct parapophyses are found in a number of fishes, as *Cristivomer*, *Alosa*.

It may be here remarked that the vertebral centra of *Tarpon* are very different from those of *Xiphactinus*, being very solid, smooth, and wholly devoid of the deep lateral grooves. Most of the neural arches have become coössified with the centra, and appearances indicate that in the young fish there were separate parapophyses, which later coalesced with the centra. The vertebral column has attained a much higher grade of development than that of *Xiphactinus*.

The specimen that I have above referred to *X. thaumas*, I believe to be such; but lest it prove to be something else I shall here attempt a description and a comparison with other species. It certainly is not *X. molossus*, since that species has the distal extremity of the maxillary upturned like a saber. Moreover, as I have already illustrated (Fig. 2), the condyles are very different from those of undoubted specimens of *X. molossus*. It cannot be *X. mudgei*, since this species possesses four subequal teeth in the premaxillary, while in my specimen there are present only two teeth. Moreover, the vertical extent of the maxillary behind the posterior condyle is too great. The specimen possibly belongs to *X. lestrio*. Cope

speaks of the two maxillary condyles of that species as being large and separated by a space. This description, though vague, would fit my specimen. But *X. lestrio* is stated to have three, and sometimes four, premaxillary teeth. As I have said, I find no evidence of a third tooth. The total length of the upper jaw of my specimen, including the premaxillary, is 380 mm. The height of the maxillary from lower border to top of posterior condyle is 125 mm., almost exactly one-third the length. Applying this proportion to Cope's figure of *X. lestrio* (*Cret. Vert.*, Pl. XLII, Fig. 1), we find that his drawing of the maxillary would have to end at the right hand within about 8 mm. beyond its present limit, in order to represent the complete bone. It is very evident that a much more considerable piece of that maxillary was wanting. Had this missing portion of that bone had the form and proportions possessed by my specimen, the drawing would have to extend 25 mm. further to the right. This would make the jaw much longer in proportion to its height than my specimen.

As a matter of fact, I find no serious discrepancy between Cope's description of his *Portheus thaumas* and my specimen. I give description of the upper jaw.

Upper jaw heavy and massive ; its height being apparently greater in proportion to its length than in other species, one to three. Premaxillary broadly oval ; its major axis 130 mm., its transverse 110 mm., its greatest thickness 40 mm. Teeth two, the most anterior projecting 55 mm. beyond the bone ; its diameter at base 20 mm. Second tooth 22 mm. long, probably not full grown. Maxillary extending forward against inner surface of premaxillary nearly to the anterior border of latter. Condyles as shown in Fig. 2. Tooth border sinuous, slightly concave just behind premaxillary suture, then convex to beyond large teeth, then again more strongly concave ; finally convex, and rounding into the distal border. Upper border descending rapidly from posterior condyle and concave to point three-fifths of distance to distal extremity, there forming an angle, and again concave until it begins to round into the distal border. In general, the distal third of the maxillary bends downward instead of upward. On dental border there are in front, first,

traces of four or five small and medium teeth, then five large teeth, two of which are yet present and projecting 40 mm., then some 40 teeth from 11 mm. in length to mere points. Extreme height of maxillary 125 mm.; its height 72 mm., at a point on upper border 125 mm. behind the anterior border of posterior condyle. This enters into the total length of the upper jaw 5.3 times, and into height at condyle 1.75 times.

I take pleasure in acknowledging my obligations to Prof. F. A. Lucas, in charge of the osteological collections of the United States National Museum, for the generous manner in which he has given me access to such materials as I have needed.



# ZOÖLOGICAL BULLETIN.

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## OBSERVATIONS ON THE ANATOMY OF A SPECIES OF PLATYASPIS FOUND PARASITIC ON THE UNIONIDAE OF LAKE CHAUTAUQUA.

HENRY LESLIE OSBORN.

THE facts recorded in this article were gathered partly on living material at Chautauqua, New York, in the Biological Laboratory of Chautauqua College of Liberal Arts, and chiefly in the Biological Laboratory of Hamline University, St. Paul, Minn. The fluke was first noticed in July, 1895, in specimens of *Anodonta* which were being used in class work. A few drawings were made at the time, but no attempt at identification could be undertaken then, as the necessary books were not at hand. Later in the year I consulted Bronn's *Klassen und Ordnungen* and decided that it could not possibly be regarded as the usual parasite of the *Unionidae* *Aspidogaster conchicola*, and recognized that it bore a remarkably close superficial resemblance to a species designated in that work as the *Aspidogaster lenoiri* of Poirier ('85). Such points as could be determined by a mere surface study of the animal indicated clearly a very decided likeness between Poirier's species and mine, but the point which made me hesitate in associating them at that time was the fact that Poirier's animal is only recorded from a single region, *viz.*, Senegal, Africa, and from a single host, *Tetrathyra vaillanti*, a *chelonian*. Unfamiliarity with the Trematoda and pressure of other work prevented me from investigating the case at that time, and I did not really take it in hand till the fall of 1897, when I was gathering the facts for a paper, Osborn ('98), on the dis-

coloration of Anodonta shells by a distomid parasite. I planned then to append the facts about *Platyaspis* to that paper in a short note. But as soon as I looked into the case I found a number of interesting points whose novel character made it necessary to present the evidences in the case in a way impossible in a mere note, and hence I withheld the matter and have made it the subject of another article. Poirier referred the animal which he discovered to the genus *Aspidogaster*, and Braun ('92) in Bronn's *Klassen und Ordnungen* followed his assignment of the animal to that genus. But Monticelli ('92), in his revision of the Aspidobothridae which accompanies the paper on *Cotylaspis* in Leukart's *Festschrift*, showed that Poirier's animal cannot be regarded as an *Aspidogaster*, and erected for it the genus *Platyaspis*, of which it has thus far been the solitary species. So far as I have been able to ascertain, *Platyaspis* has never been recognized, excepting from the one locality in which Poirier found and described it. It is, consequently, an interesting and remarkable fact that it should occur in this country and in a very different host, and a fact which should not be presented without a sufficiently detailed account of the evidence to compel belief in the correctness of the observation.

I have not been able to decide in my own mind whether the Chautauqua animal is specifically distinct from the African species or not. This is partly because I have not as yet had access to the original descriptions of Poirier, and do not know how absolutely exact his account and the reports of them are. The Chautauqua animal is slightly different from his, but not more so than might be consistent with membership in the same species. In case the Chautauqua animal proves to be distinct, I shall propose for it the name *Platyaspis anodontae*, and for convenience shall so term it in this article.

The facts which are contributed in this paper are derived from studies of preserved material made in the Biological Laboratory of Hamline University. At the time of their discovery I made sketches of the living animals, but did not attempt to study them in detail. Last summer I preserved a few by dropping them into cold saturated aqueous corrosive sublimate solution. The material has its limitations, but is sufficiently well

preserved to enable one, by making total preparations and by serial sectionizing, to recognize all the most important anatomical features of the animal, and, in addition, to see histological detail enough to supplement the anatomical identification of the organs. But I have not been able to demonstrate on the preserved material the exact relation of the different members of the reproductive system, or to follow out the branchings of the excretory system. This, and a more careful study of the histology, I hope to make during the coming summer with the aid of living material. In the meantime I will report the facts as already determined.

I have had only a partial access to the literature of the subject, but gladly acknowledge my especial indebtedness to Monticelli's article in Leukart's Festschrift, in which he gives some account with illustrations of *Platyaspis*, and to Stafford's article on *Aspidogaster*. These and other articles referred to are indicated at the conclusion of this paper. I am also much indebted to Dr. W. S. Nickerson of the University of Minnesota, for the privilege of examining his trematode preparations and for friendly advice as to methods of trematode study.

#### HABITS.

*P. anodontae* is habitually, if not exclusively, found, not in the pericardial chamber or cavities of the nephridium, but in the mantle chamber, where it is attached either to the surface of the visceral mass, the inner surface of the gill, or to the under surface of the kidney, where the mantle and cloacal chambers communicate anteriorly. While I have not made a sufficiently complete search to be able to assert that it is never located inside of the pericardial chamber or kidney, I feel confident that if it is found there that position is not habitual. This point will receive particular attention in my later work. In its location *P. anodontae* is thus ectoparasitic, and hence decidedly unlike *Aspidogaster*, which, according to authors, is habitually found inside the pericardial cavity and nephridium. Thus Stafford ('96), p. 8, says: "On opening the *Anodonta* the parasites are often visible in the transparent pericardium. It

was in this organ that the great mass of Aspidogasters was obtained ; and, generally, they were found closely packed into the anterior corners, at the entrance into the kidney and pericardial gland. In these latter organs I have found a good number, too, but in no other organ have I succeeded in finding any, although I have taken considerable trouble to find evidence of the migration of the young animals." And a similar impression is given by Huxley ('72), Hoyle, *Encyclopaedia Britannica*, XXIII, p. 540, and Monticelli ('92), as well as in most of the current text-books, etc.

Its situation is also quite unlike that attributed by Poirier to *Platyaspis lenoiri*, which is an internal parasite of the turtle. We do not know that *Platyaspis* does not have two hosts, but the supposition is unlikely in view of the habits of the family Aspidobothridae, and if it should prove to be the fact that it has only one, then these two *Platyaspid* forms are very different indeed in their host relations.

I am not prepared at present to say much about the host distribution of the parasite, but I can say that in Lake Chautauqua it is chiefly but not absolutely confined to *Anodonta*. The following Unionidae have been recognized growing in close proximity : *Anodonta plana* Lea, *Unio luteolus* Lam, *U. edentula*, *U. phaseolus* Hld., *U. gibbosus* Brns.; and while *Anodonta* seems to be the most usual host, the parasite has been noticed rarely in *U. luteolus*. I have not met with *Aspidogaster* at Lake Chautauqua, but as it is an endoparasite it may easily be present there and have escaped my notice, since I have not made a point of searching carefully through the pericardium and other organs in which it is reported as likely to occur. I do not, however, imagine that it is very common, for, in case it were, it would surely have attracted attention during the many dissections that have been made by the students.

I have not as yet made a strict study of the habits of the parasite. On opening the mantle cavity of the host in air, one of course subjects the parasite to very unnatural conditions; at such time it adheres to the surface of the host by means of its enormous and highly complex ventral sucker, and its anterior



end is moved in an exploring sort of way. Under compression the anterior end is seen to be very mobile, assuming successively an immense number of apparently random shapes with great rapidity and ease.

#### EXTERNAL ANATOMY.

The individuals externally resemble (see Figs. 1-3) the form represented in Bronn and Monticelli for *P. lenoiri* so exactly that at the outset I was hardly sure that the animals

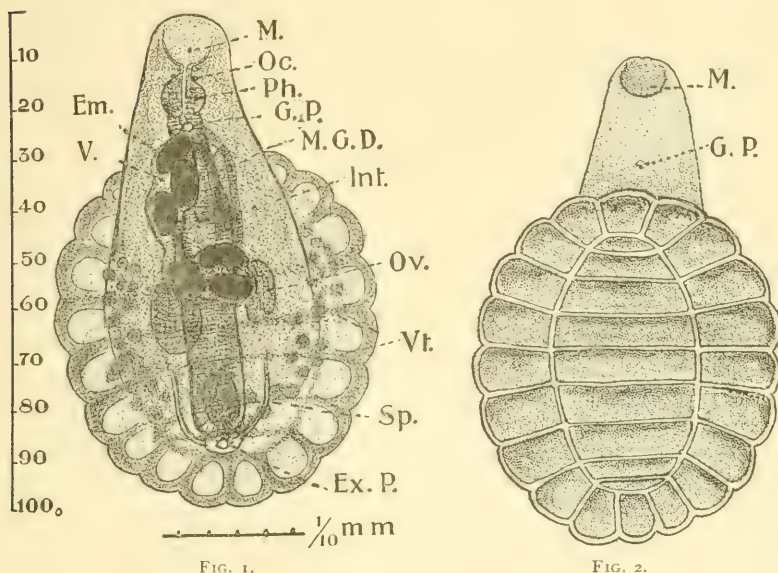


FIG. 1.—Camera lucida dorsal view of *P. anodontae* as a transparent object, made from a total preparation in Canada balsam, and by reconstruction from serial sections.

FIG. 2.—Surface view of the ventral surface of *P. anodontae*, drawn with a camera lucida. The genital opening was not seen in the animal, but is introduced from the sections (camera lucida).

are specifically distinct. There is a division of the body into two parts (see Fig. 3), an anterior and dorsal tubular elongate body, resting upon a broad, flat ventral and posterior portion,

<sup>1</sup> The following reference letters are used in all the figures: D., Diaphragm; Em., Embryos; Ex. P., Excretory pore; G. P., Genital pore; Int., Intestine; M., Mouth; M. G. D., Male genital duct; Nv., Nerve trunk; Oc., Eye; Ov., Ovary; P., Parenchyma; Sp., Spermary; V., Vagina; Vt., Vitellaria.

much after the fashion of the relation of a snail's body to its foot. These divisions are maintained internally to a considerable extent, as will be seen later, the alimentary and excretory systems being confined to the body, or "neck," as the dorsal tubular portion is called, while the reproductive system is largely located in the ventral and expanded "foot." The entire length of the animal from the tip of the foot behind to the tip of the neck in front (in an alcoholic specimen) was, in one case, 1.6 mm. ; Monticelli gives 1.7 mm. for *P. lenoiri*. The foot, or ventral sucker, is 1.3 mm. long and 1 mm. broad, and is thus the most prominent external feature of the animal.



FIG. 3. — Side view of *P. anodontae*, showing the "neck" rising from the broad foot.

There is no differentiated oral sucker, the wall of the body at the anterior end being thin and delicate and strikingly (see Fig. 4) unlike the much thickened condition found in Distomids, and generally in the trematodes, where a distinct oral sucker is present. The generative opening (Fig. 1, G. P.) is located in the middle ventral line, near the junction of the anterior region with the foot. The hinder broadened portion of the animal consists of a dorsal portion which shades down imperceptibly laterally and posteriorly from the tubular anterior portion and fades out posteriorly to form the broad, flat dorsal surface of the sucker. This latter extends into an extremely thin rim all around the edge of the foot, and includes a flap which extends in front of the junction of the sucker with the anterior region of the body. On the hinder dorsal surface of the body, near the extreme posterior end, is located the opening of the excretory system (Fig. 1, Ex. P.).

The ventral sucker itself is subdivided, the plan of its subdivisions being entirely unlike that of *Aspidogaster*, and as distinctly similar to that of *Platyaspis*. The surface of the sucker (see Fig. 2) is regularly subdivided by transverse and longitudinal folds into compartments, of which there is a distinct peripheral series of 20 compartments and a median series of 9, making 29 compartments in all. The precise position of the

ridges which border these compartments is shown in the camera lucida drawing of the ventral surface. This number of compartments is different from that given by authors for *P. lenoiri*, where there are 25 compartments, 18 in the peripheral series, and only 7 in the median row, in place of 20 in the peripheral and 9 in the median row, as here. I have, however, not determined how constant the plan of this subdivision of the ventral sucker is, but I have found the number given in my figure in about twenty cases.

#### INTERNAL ANATOMY.

The animal is covered with the usual trematode body wall, consisting of a thin and delicate cuticle, beneath which, in sections, the ends of muscle fibers are recognizable. Internally

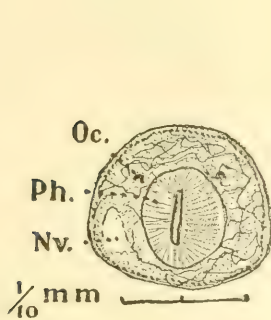


FIG. 4.

FIG. 4. — Transverse section, passing through the eyes, level Oc. in Fig. 1, No. 12 of series (camera lucida).

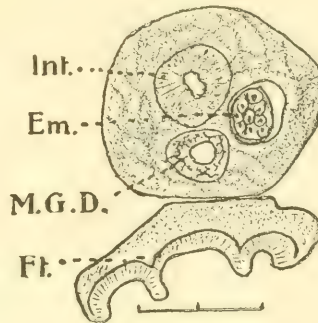


FIG. 5.

FIG. 5. — Transverse section, No. 31 of series. The left of the section is the right side of the animal (camera lucida).

the inter-spaces between the organs are filled in with the usual parenchymatous tissue. This is subdivided into that of the body and that of the foot by a transverse diaphragm, as seen in Fig. 6. The alimentary and excretory systems lie wholly dorsal to this structure, as well as the terminal ducts of the reproductive system, while the gonads themselves, and the vitellaria, are wholly ventral to the diaphragm.

The alimentary system begins with a widely dilatable funnel-shaped "pre-pharynx," surrounded by the extremely mobile and

thin-walled homologue of the oral sucker. This narrows rapidly posteriorly and leads into a pharynx, oval in outline, and composed of muscular tissue and cuticularized on its outer surface. Posterior to this chamber there is, as in *Aspidogaster* (Stafford, Fig. 1) and *Stichocotyle*, Nickerson ('94), a very short oesophagus, whose wall is cuticularized and not glandular, followed immediately by a single, rather large tube, the intestine. This runs down the body to near the posterior end (section No. 88 of Fig. 1), where it ends on the same level as the opening of the

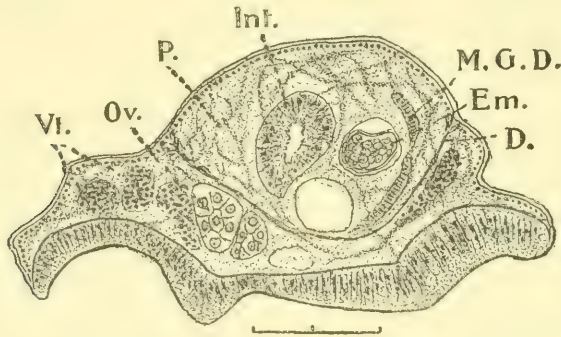


FIG. 6.—Transverse section of *P. anodontae*, serial No. 54, passing through the ovary. The right side of the figure is the left of the animal (camera lucida).

excretory system. This tube has a uniform diameter (see Int., Figs. 5, 6), and is lined with tall glandular cells, which are, many of them, peculiarly vacuolated at the outer end (*i.e.*, next the surface of the membrane), as noted by Nickerson in *Stichocotyle*.

The excretory system was only recognized in sections, and, as to its terminal portions, its minor divisions, and their relations to the inter-spaces of the parenchyma, must be studied upon living specimens. The excretory pore is clearly visible in sections and in surface views of total preparations. It is located in section No. 83, and it is a single opening, and not double, as reported for *Aspidogaster* by Stafford. The sections on which this conclusion rests are not shown in this article, but will be given in connection with my later paper. Two enlarged terminal collecting excretory vesicles are seen meeting beneath the surface pore in horizontal sections. They can be traced forwards on either side, but ultimately they are lost in the parenchyma. These points are indicated in Fig. 1.



The nervous system was only imperfectly seen. I did not recognize it at all in the living animals, and it barely shows in the total preparations, but in transverse sections it is clear that there is a large band of fibers crossing the pharynx dorsally—far forward (in section No. 10), and extending down ventrally around the pharynx so as to more than half encircle it. A lateral nerve can be traced posteriorly in a few sections. It shows at Nv. in Fig. 4.

Just posterior to this nerve band there are located two symmetrically disposed organs. They are shown at Oc. in Figs. 1 and 4, where their location is indicated. They are, apparently, invariable structures, very noticeable in living animals, and I have found them in every individual that I have examined without any exception. They are spherical bodies located in the parenchyma, deeply below the surface and near the anterior boundary of the pharynx; they are posterior and close to the cerebral nerve mass. They are spherical and apparently hollow. The surface is pigmented; the pigment, in the form of minute grains, is clearly visible under the immersion lens; these grains are, apparently, scattered on all parts of the surface of the sphere, but they are much more closely deposited on the inner and upper side. I have not thus far recognized any lens. I have from the first considered them eyes; their invariable presence, their position in the neighborhood of the cerebral nerve mass, and the presence of pigment demanding this identification. If, however, we accept them as eyes, we must recognize that *P. anodontae* differs in possessing them from adult trematodes generally. It is well known that eyes are present in early stages of the trematodes, but they are not hitherto recorded of adults, so far as I am able to learn. The accounts of *P. lenoiri* do not mention this point, and the illustrations do not shed any light on the question; so far as can be ascertained from them, these organs are wanting in the African form. There is no room for doubt as to the Chautauqua animals being adult; the condition of the reproductive system at large and the presence of eggs and embryos settle that. It is, perhaps, hardly worth while to speculate on the matter now, but I cannot help noting the possible correlation between

the comparatively free life of *P. anodontae* and the possession of eyes, in contrast with the absence of eyes in the strictly endoparasitic *P. lenoiri* and its allies, the other genera of this family.

The location of the chief organs of the reproductive system agrees closely with that indicated for *P. lenoiri* in the figure in Bronn (Pl. XX, Fig. 1); and it is also very similar to the arrangements found in *Aspidogaster*. I have not been able to trace all of the windings of the ducts by the section method; their intricacy has made it impossible to do so; but I feel reasonably sure of the identification of the portions which I have introduced into the partially diagrammatic Fig. 1. The spermary is single. It is recognized by the presence of small spermatic cells, but no spermatozoa were recognized in any of the sections. The organ is oval, large, and located about on a level with the hind end of the intestine, and ventrally to it. The nuclear material indicated, possibly, some activity in the tissue, but no mitotic figures were visible. I have thought of two suppositions by which to account for their absence, *viz.*, the organs may not have been in a state of activity at the time; and, second, the methods of preservation may not have been adequate. I found in staining that the presence of the cuticle interfered with the action of reagents, and it is quite possible that the germinal cells, if active, got into a state of rest before the reagent used in fixation had had time to take effect. The almost invariable presence of the embryos in the vagina seems to indicate that the animal is mature and that, consequently, these organs are or have been active.

There is a single ovary. It lies on the right side of the body (see Figs. 1 and 6), near the middle, and ventrally to the intestine, and below the diaphragm. The vitellaria are also conspicuous, lying scattered through the ventral portion of the flattened body, near its margin. I have not as yet succeeded in tracing the ducts which connect the different portions of the female reproductive organs. The terminal portions of the reproductive system have been identified with reasonable certainty. The generative opening is visible in the mid-ventral line of section No. 23. This places it in front of the foot, in

the position indicated in Fig. 2, the same position as that assigned to it in *P. lenoiri*, in *Aspidogaster*, and in *Stichocotyle*. Two distinct passages lead posteriorly from this common opening, the male and the female ducts. These have not been followed back so as to enable me to base their identification upon a connection, respectively, with the spermary and ovary. However, I feel tolerably sure that the one on the right side is the male passage and that on the left the female, as indicated in Fig. 1. The latter contains a small number of oval chitin-enclosed capsules, usually about six, which I am inclined to regard as embryos. They are conspicuous in total preparations, and in sections the chitinous capsule is seen surrounding a mass of protoplasmic nucleated cells. These objects are, apparently, identical with similar structures located in the passage leading to the uterus in Poirier's figure (Pl. XX, Fig. 1). According to that figure the passage is one which leads directly from the ovary, and receives a duct from the yolk gland and vitellaria in its course. The objects in the duct are very different indeed from the embryos of most flukes, including the innumerable small embryos of the closely allied *Aspidogaster*; but their situation and their chitinous covering are so identical with those of the fluke embryos at large that there can be no doubt that these are embryos, but extremely interesting from their unusual size. It is obvious that in *Platyaspis* we have to do, not with an immense number of small embryos, as in the flukes generally, but with a few large ones.

If we accept the view that these objects are embryos, we are then able to identify the passage containing them as the vagina, an identification which locates that organ as it is located in *P. lenoiri* and *Aspidogaster*, but not in *Stichocotyle*, where it is on the right side (Nickerson, '94, p. 477). I might add that it is some additional evidence in favor of this identification that the wall of the organ agrees histologically with that of the homologous organ of *Aspidogaster*.

The other of the two passages opening at the genital pore is thus indicated to be the cirrus organ, the terminal portion of the spermiduct. In favor of this view, in addition to the points mentioned in connection with the identification of the other as

the oviduct, is its histological structure, which closely resembles that indicated by Stafford for *Aspidogaster*.

#### SYSTEMATIC POSITION.

The question of the systematic position of the *Chautauqua* *Platyaspis* does not at present admit of a final answer. There can be no doubt of its generic position. Its anatomy agrees so completely with *P. lenoiri* in all essential particulars, and is so completely unlike that of the other genera of the *Aspidobothridae* in all generic points, that it can, I think, be finally stated that it is a species of *Platyaspis*.

The only divergences thus far recognized from Poirier's species *P. lenoiri* are in the number of the compartments of the ventral sucker and in the presence of eyes. As for the first of these, it would be necessary to study the case of the American species more fully to determine whether the number of compartments is a constant feature; so far as is at present known it is constant. And it would be necessary to study the African species as well, to determine whether the account of Poirier is to be regarded as absolutely and exactly true and invariable. If such should prove to be the case, it would furnish good grounds for regarding the American form as specifically distinct. As for the point about the presence of the eyes in one case and their absence in the other, it is possible that the organs are not functional eyes, but only rudiments, which are more distinct in the American form than in the African. They may be present in the African form, but less distinct, and so may have escaped notice. At all events, it is at present impossible to decide that the animals are specifically distinct. Still, since they are so widely apart in home and habit, at least so far as our present knowledge of them goes, it appears, on the whole, best to recognize them by distinct names.



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BIOLOGICAL LABORATORY OF HAMLINE UNIVERSITY,

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## THE EMBRYOLOGY OF THE APTERYGOTA.

AGNES M. CLAYPOLE, PH.D.

UP to within the last few years comparatively little work has been done on the embryology of the lowly insect forms included in Brauer's group Apterygota, and until we reach the recent date of 1892 no studies of serial sections have been reported. Hence there are among earlier works many misinterpretations of superficial features. Much of the early work was done on members of the subdivision Collembola, including the more lowly apterygote insects. The first contribution came from the systematist Nicolet. Unfortunately, but meager data of this article have been obtained. It can merely be stated that some time previous to 1869 Nicolet published studies on *Podura aquatica*, *Desoria cinerea*, *Cyphodeirus agilis*, *Sminthurus ornatus*, and *Orchesella* sp(?). He established three facts: that holoblastic cleavage exists among the Collembola; that their eggs are spherical; that an amnion and serosa are wanting.

In 1871 Packard<sup>1</sup> gave the results of studies on the form *Isotoma walkeri*, not a thysanuran, but a collembolan. Only the stages after germ-band formation are mentioned. This is said to arise as a complete girdle and to show early 6-7 segments. These were identified as antennae 1, mandibles 1, maxillae 1, with possibly a second, thoracic legs 3. Later rudiments of a spring appear on the fifth abdominal segment; an unpaired median labrum is also developed. At no time are any tracheae present, and the larvae on leaving the egg resemble the lower Collembola more than the adult *Isotoma*. A cuticle like that of crustaceans appears during development.

In 1875 Oulganine<sup>2</sup> published studies on *Achorutes tuberculatus* Nic., *Anurophorus fimetarius*, and two species of *Degeeria*.

<sup>1</sup> Packard, Jr., A. S., "Embryological Studies on Diplax, Perithemis, and the Thysanurous Genus *Isotoma*," *Peabody Acad. Sci.* No. 11. 1871.

<sup>2</sup> Oulganine, W., "Sur le Développement des Podurelles" (Extrait du Russe par M. de Korotneff), *Arch. de Zool. Exper.* Tome iv. 1875.

The eggs all undergo equal holoblastic cleavage, resulting in a uniform single-layered blastoderm soon rendered many layered by rapid growth. The surface becomes crenated and ridged and forms a cuticle, also crenated. The blastoderm becomes smooth, and outlines of the embryo appear. The second embryonic layer is said to arise from a definitely placed area lying between the head and tail of the belt-like germ band. A "dorsal organ" is probably present, though not described as such. Nine pairs of appendages appear: antennae 1, mandibles 1, maxillae 2, thoracic legs 3, abdominal 2. One pair of those on the abdomen forms the colophore, and the other the spring. Poduridae are found to resemble the lower arthropods in the following respects: (1) holoblastic cleavage; (2) absence of amnion; (3) possession of blastodermic cuticles; (4) the formation of the intestine from the middle germ layer.

In 1882 Lemoine<sup>3</sup> added studies on the Collembola *Anurophorus laricis* and *Sminthurus plumbeus*, two species differing widely from each other in habits and form. The first is small, springless, inactive, and colonial, while the second is large, with a well-developed spring, active, and solitary. The eggs of *Anurophorus* found in April and May were clear and easy to observe, while those of *Sminthurus* found in November and December were slow in development and difficult to study. Superficial cleavage, accompanied by secondary yolk cleavage, was true of the former, and the latter showed very unequal holoblastic cleavage with a blastoderm early formed of two layers. "Dorsal organs" appear in both, persisting up to the time of hatching. The entoderm is said to arise from two inpittings, one in front and one behind the "dorsal organ" and at several other places on the periphery. The germ band, at first forming a belt surrounding the whole circumference of the egg, shows 12-13 segments: 1 cephalic, 3 mandibular, 3 thoracic, and 5-6 abdominal. Two membranes appear, one of which is clearly connected with the "dorsal organ." A colophore develops in both forms, but the spring is rudimentary in *Anurophorus*, a condition also true of the tracheal system.

<sup>3</sup> Lemoine, P., "Recherches sur le Développement des Podurelles," *Ass. Franc. p. avanc. des Sci.* La Rochelle. 1882.



Grassi<sup>4</sup> gives the first mention of thysanuran development. He describes three features in the developmental processes of Japyx. The cleavage is distinctly superficial; an amnion exists, and also a "dorsal organ."

Ryder<sup>5</sup> published studies on *Anurida maritima* Guen., giving the following results. After the formation of the germ band two membranes invest the embryo, the inner one being crenated. The embryonic area forms a nearly complete belt surrounding the egg, and seven pairs of appendages can be made out: antennae 1, mandibles 1, maxillae 1, thoracic legs 3, and the colophore on the first abdominal segment. A rudimentary spring is reported as still visible on the fourth abdominal segment of the hatched larva, but no trace remains in the adult.

Wheeler<sup>6</sup> gives the first account of section views of an apterygote insect. He shows the existence of an intercalary segment with appendages in the head of *Anurida maritima*, placed between the mandibular and antennal segments. The "dorsal organ" is shown in section and is definitely homologized with the "indusium" of Xiphidium.

Later studies all include internal structure as seen in sections. In 1896 Heymons<sup>7</sup> published a short account of his work on *Lepisma saccharina*, the highest of the Thysanura. The eggs of this species are oval and about 1 mm. in their longest diameter; cleavage is distinctly superficial, and an extremely small germ band early appears. This is found to sink immediately into the yolk, still, however, retaining its connection with the serosa, the extraembryonic part of the blastoderm, by a thin membrane, the amnion. As the embryo sinks in, the amniotic cavity becomes large and distinct, but always retains connection with the outside by the open amnion pore. The amnion is hence never constricted from the serosa. By later growth of the germ band the pore is opened and the amnion is retracted

<sup>4</sup> Grassi, B., "I Progenitori degli Insetti e dei Miriapodi l'Japyx e la Campo-dea," *Atti accad. Gioenia Sci. Nat. in Catania*. (3), vol. xix. 1885.

<sup>5</sup> Ryder, J. A., "The Embryology of *Anurida Maritima* Guen.," *Amer. Nat.* Vol. xx. 1888.

<sup>6</sup> Wheeler, W. M., "A Contribution to Insect Embryology," *Journ. of Morph.* Vol. viii, No. 1. 1893.

<sup>7</sup> Heymons, R., "Ein Beitrag zur Entwicklungsgeschichte der Insekten Apterygota," *Sitz. Berichte Acad. Wiss.* Berlin. 1896.

to form a "dorsal organ" similar to the structure of that name in the pterygote insect. The author proves two points: (1) that Thysanuran cleavage is superficial, differing from the Collembolean type, and (2) that embryonic membranes are formed homologous with those of the Pterygota. Hence *Lepisma* is an intermediate form transitional between the *Collembola* and higher insects.

This paper is followed in 1897 by a longer and more complete study of the same form at the hands of the same worker, Heymons.<sup>8</sup> In this he shows that some of the cleavage nuclei migrate from the center to form the blastoderm, while others remain in the yolk as yolk-cells. The gastrula has the form of a circular depression instead of the typical groove, and as soon as a two-layered condition is attained the germ band sinks into the yolk. While buried in the yolk the germ-band segments and paired appendages appear. First antennae, post-oral in position, next distinct intercalary appendages, mandibles, and two pairs of maxillae with a median unpaired labrum. The maxillae early split in two longitudinally, and the maxillary palps remain clearly homologous with the thoracic legs. Paired abdominal appendages appear on each segment except the 11th, getting progressively smaller from the first pair to the 10th. After several weeks the larvae hatch and are chiefly distinguished from the adults by their white color and the absence of the styli and cerci.

The reproductive cells appear at an early stage in the hind end of the embryo and are clearly of ectodermic origin; after much migrating they enter the primitive somites and form follicles segmentally arranged in the female. The mesenteron was described as arising from yolk-cells that migrate from the yolk and multiply to form a continuous layer enclosing the yolk and is hence entodermal in origin. In conclusion it is clear that the Thysanura show strongly marked pterygote peculiarities, and the conditions described suggest the author's opinion that the formation of embryonic envelopes is due to increase of yolk material in the egg.

<sup>8</sup> Heymons, R., "Entwicklungsgeschichtliche Untersuchungen an *Lepisma saccharina* L.," *Zeitschr. f. wiss. Zool.* Bd. lxii. 1897.

At almost the same time Uzel<sup>9</sup> published a series of articles on the two forms Campodea and Lepisma. His work on the latter practically confirms that of Heymons and may be omitted from this review. He determines that the eggs of Campodea are spherical, about 0.4 mm. in diameter, undergo superficial cleavage, resulting in a blastoderm spread uniformly over the whole surface. No secondary yolk cleavage exists. The germ band arises by migration of cells from all parts of the blastoderm to form a belt encircling nearly the whole egg. A "dorsal organ" appears between the head and the tail, but neither an amnion nor a serosa is developed. Paired appendages are early distinguished, also a median unpaired labrum. Of the paired appendages the following are found: one pair of antennae, a pair of distinct intercalary appendages, one pair of mandibles, two pairs of maxillae, three pairs of thoracic feet, and nine pairs of abdominal structures. An interesting point is noted in the permanent retention of the intercalary appendages as lateral folds round the adult mouth. Later the 1-7th abdominal appendages split longitudinally, the outer part forming the permanent styli and the inner the abdominal sacs.

There is to appear in the new *Journal of Morphology*<sup>10</sup> a paper giving the results of my studies on *Anurida maritima*. Merely a summary of the most important points will be included in this consideration. It was found that the ovary was extremely simple in form, like that of a myriapod. Each ovum is associated with nutritive cells and the germinal vesicle early disappears. The egg is spherical, about .27 mm. in diameter, with at first slightly unequal holoblastic cleavage; this is eventually lost after a large-celled morula stage has been formed, and the blastoderm rises by migration, as in eggs with superficial cleavage. It assumes a two-layered condition at once, the entoderm remaining dormant in the yolk. A "dorsal organ" is formed between the two ends of the belt-like germ band, the latter early showing the usual pairs of appendages

<sup>9</sup> Uzel, H., "Vorläufige Mittheilungen über die Entwicklung der Thysanura. Beiträge zur Entwicklungsgeschichte von Campodea staphilinus," *Zool. Anz.* Nrs. 125, 128, 135. 1877.

<sup>10</sup> Claypole, A. M., "The Oögenesis and Embryology of *Anurida Maritima*," *Journ. of Morph.* Vol. xiv. 1898.

together with a pair on the intercalary segment which takes part in the formation of the adult mouth. These are homologized with the second pair of Crustacean antennae. Yolk is found enclosed with reproductive cells, causing their very rapid development. Anurida agrees with the rest of the Collembola in showing characters allying it strongly with the lower arthropods.

Summing up the present state of knowledge regarding Apterygote embryology, it is found that at least fourteen species of Collembola and three of Thysanura have been studied with more or less care. This work confirms by its results the opinion that the Apterygota possess truly primitive characters and also show transitions to the higher and lower Arthropoda. Cleavage among the Collembola, as far as determined, shows many types: equal holoblastic, unequal holoblastic, holoblastic becoming superficial, and truly superficial; while on the other hand the Thysanura show only the superficial type, whether the eggs are spherical or oval. It is unfortunate that in most cases the size of the eggs is not given, and in many instances the method of cleavage is unknown. Still a comparison of the three available forms is instructive.

ANURIDA. Spherical, .27 mm. in diameter. Cleavage holoblastic becoming superficial.

CAMPODEA. Spherical, .4 mm. Superficial cleavage.

LEPISMA. Oval, 1. mm. Superficial cleavage.

The apparent discrepancy between the two sizes given for the eggs of Anurida by Ryder and myself is readily explained by the fact that the measurements were taken at different stages. There is a marked increase in size during development. No early stages are described for Isotoma, whose size is the smallest yet recorded (.15 mm.), but some of Packard's so-called germ-band figures suggest strongly that they are possibly stages showing the first cleavage plane appearing. Enough is given in this short series to indicate a regular increase in the size of the egg and a *pari passu* loss of holoblastic cleavage in passing up the scale of apterygote insects. The only trace of the total cleavage remaining in Lepisma is shown in the yolk



cleavage; it is markedly significant that nothing of this kind occurs in Anurida after the holoblastic condition is lost, though the yolk is fused into a solid mass and nuclei are scattered through it; such secondary cleavage is reported in Anurophorus, where egg cleavage is superficial.

It is equally clear that the amnion and serosa are absent in the Collembola, the embryonic membranes formed having the nature of "Blastodermhäuten." In Anurophorus, Achorutes, Degeeria, Sminthurus, and Anurida these membranes show some amount of crenation and hence have powers of expansion. In all cases they are found in connection with the so-called "dorsal organ," which is a structure clearly homologous throughout the Collembola, being similarly placed and similar in development. A similar structure, similarly placed, is also found in Campodea and Japyx. Heymons considers the "dorsal organ," caused by the invaginating cellula envelopes, homologous with these. But the distinct and early appearance of this organ and the simultaneous presence of the amnion and serosa in Japyx and Campodea are clear evidences against such an homology. This is still further confirmed by reference to the structure described by Wheeler as the "indusium"; this is without doubt, as he states, the homologue of the apterygote "dorsal organ," and is certainly distinct from the structure that rises later during the elimination of embryonic envelopes. It is possible that a structure similar to the earlier stages of the indusium may exist in Lepisma, but no such specialized later developments would be expected as those found in the Orthoptera.

It is also interesting to see the clearness with which certain facts are indicated as to the appearance and fate of certain appendages. The colophore is without doubt a fused pair of abdominal feet; the spring has a similar origin on the fourth or fifth abdominal segment, and according to Uzel the styli and ventral bladders rise directly from abdominal appendages. There is almost unanimous evidence that an intercalary segment exists in the apterygote head placed between the antennae and the mandibles, disappearing in some cases but remaining to form permanent mouth-parts in others. It is reasonable to

consider them the homologues of the second pair of Crustacean antennae.

In every way the apterygote insect appears to be truly primitive ; no evidences of wings appear, and many points in shape of eggs, cleavage, embryonic membranes, and appendages show resemblances to the lower Arthropoda. One question has been purposely left untouched in this brief review : that of gastrulation. It is only from studies based on sections that safe conclusions can be drawn, and the difficulties introduced by the method of germ-layer formation described for Anurida render further facts necessary concerning these processes in other forms before general principles can be safely deduced.

WELLESLEY COLLEGE,  
WELLESLEY, MASS.

A FEW FACTS CONCERNING THE RELATION-  
SHIPS AND REPRODUCTION OF SOME  
BERING SEA TUNICATES.

WM. E. RITTER.

WHILE President Jordan was engaged, as commissioner in charge of the fur-seal investigations for 1896, in studying the natural history of the seals of the Pribilof Islands, he collected a considerable number of tunicates. These he kindly intrusted to me for study. They proved to be so interesting that during his second summer's work (1897) in the same capacity he encouraged the enthusiastic young zoölogists, R. E. Snodgrass, A. W. Greeley, and Trevor Kincaid, who accompanied him, to give particular attention to collecting these animals. The result was a large, well-preserved collection, the study of which contributes substantially, in several directions, to our knowledge of the group. These contributions will appear in detail as a part of the final report of the scientific investigations made by the commission, to be published later by the United States Government. Some of the facts brought to light are, however, of sufficient consequence to make worth while their publication in advance of the report itself. I consequently present them here. As indicated by the title of the note, they relate to the affinities of the Bering Sea tunicate fauna and to the reproduction of some of the species studied.

The collection contains eleven species, ten of which are new to science. These are distributed among seven genera in the following way: *Boltenia*, *Styela*, *Aplidiopsis*, and *Synoicum*, each one species; *Dendrodoa* and *Polyclinum*, each two species; and *Amaroucium*, three species. So far as I am able to determine, no tunicates have before now been described from this portion of the world, the northern species hitherto known having come from the North Atlantic and Arctic oceans, mostly

from the vicinity of the Scandinavian peninsula. The addition of these species to the others already known from far northern seas increases quite to a certainty the probability that there is a distinct Arctic tunicate fauna. The clearest indication of this is afforded by the presence in the collection of the species of the genera *Dendrodoa* and *Synoicum*. The single species of the first-mentioned genus hitherto known was described by MacLeay in 1824 from Winter Island (north of British America). Herdman has expressed doubt as to whether or not MacLeay's genus is really distinct from *Styela*. From the two species now at hand I have convinced myself that the genus is thoroughly valid — much more so than many others that receive general recognition. This, then, appears to be one characteristically Arctic genus. The other genus above mentioned, *Synoicum*, seems to be quite as characteristically Arctic. The first species belonging to it was made known by Phipps (1774), and more fully described by Savigny in 1816, and came from Spitzbergen. Since then another species from Lofoten Islands, north coast of Norway, has been described by Sars. This, then, seems to be another genus characteristically northern.

Of the other species the one belonging to the genus *Aplidiopsis* has its nearest ally in *A. sarsii* Huitfeldt-Kaas, from Lofoten; and two of the three species of *Amaroucium* appear to be more closely related to *A. mutable* Sars, from Hamarfest, Norway, than to any other member of this large genus. The one representative of the genus *Boltenia* I identify as *B. elegans* Herdman, from the north Atlantic; so that six of the eleven species may be said to be characteristically far northern, three of them very pronouncedly so, they belonging to genera that are exclusively of this character. The genera *Polyclinum* and *Amaroucium* are both cosmopolitan in their distribution; they are almost sure to be represented in any considerable collection of compound ascidians from any part of the world, so that it is only by comparing among themselves the different species in each genus that anything significant as to distribution can be learned.



The facts which I here present relating to reproduction pertain to *Synoicum*<sup>1</sup> alone. They are, in outline, as follows:

On examination the colonies are found to contain zooids in various stages of degeneration, as well as those in a normal condition. Some of these degenerating individuals are without the thorax; others, again, are lacking both thorax and intestinal loop, the post-abdomen alone being present, this latter, however, retaining quite its normal form and structure. In still other zooids the post-abdomen, which alone remains, is reduced from its original club shape to a spherical form.

The post-abdomen, as with all the polyclinidae, lodges the heart, the epicardiac tubes, the sexual organs, and a variable quantity of mesenchymatous tissue, the cells of which contain a characteristic granular material which apparently is food yolk. This last-mentioned substance constitutes, in this species, by far the major portion of the bulk of the post-abdomen at the time when the latter becomes free from the rest of the zooid.

The ova at this time appear to be all contained in the compact band-shaped ovary, and are in many stages of growth. They are all, excepting the very largest, almost entirely free of yolk; they possess neither recognizable follicular epithelium nor "test" cells, and *they are distinctly amoeboid in form*. Careful examination of the ova discovers that many of them, particularly the larger ones, contain within the substance of the cytoplasm other cells in various stages of disintegration. They are ingesting other cells; they are clearly amoeboid in habit as well as in form.

Beside the amoeboid ova contained in the ovary there occur, in some of the post-abdomens that have become more nearly spherical in form, ova in which the amoeboid character is wholly wanting, they being quite spherical in form and regular in outline. In these ova, which are also considerably larger than the largest amoeboid ovarian ova, the cytoplasm is no

<sup>1</sup> *Synoicum* is a compound ascidian in which the colony is composed of a number of lobes arising from a common basal mass. Each of these lobes consists of a groundwork, or matrix, of firm, homogeneous testicular substance, in which are imbedded a small number of zooids.

longer homogeneous and clear, but is filled with granular substance. In some of these last-described ova the nucleus still maintains the large, clear, spherical, vesicular character which it presents throughout the amoeboid period. In others, however, it is indistinguishable. This last condition probably indicates the period of maturation.

In addition to these several stages of development of the ovarian ova, numerous stages, from the two-celled stage onward, in the development of the embryos have been found.

Finally there occur numerous packages of tadpoles, each package containing from ten to sixteen or more individuals, situated in cavities of the semi-cartilaginous test of the colonies. These cavities are almost perfectly spherical, are remote from the surface of the colonies, and are entirely closed. They contain nothing but the closely packed tadpoles; and after these have been picked out the firm, smooth walls of the cavities remind one of bullet molds.

The tadpoles themselves are enveloped by an unusually thick layer of what in all probability corresponds to the test formed at an early time in the embryonal life of all ascidians. But it contains an unusual number of cells, and in addition bodies of various kinds, which I can account for in no other way than by supposing them to be remnants of the parental zooids which produced the ova.

In fact, there is little room for doubt about the nature of some of them. Thus, in one instance in particular, a small cluster of them resembled the large yolk containing mesenchyme bodies of the adult zooids so strikingly that I should not have thought of questioning their nature but for the remarkable position in which they occurred.

Besides these bodies, pieces of fibers are found which are almost certainly remnants of the muscle fibers of the paternal mantle.

In some instances the tadpoles are in an advanced stage of metamorphosis while still contained in the cavities.

Mature spermatozoa, as well as others in various stages of development, are abundant in most, if not in all, of the post-abdomens.

Unfortunately, the collection does not contain sufficient specimens of this species to enable me to answer several questions of fact that arise from a consideration of the observations presented. However, the facts that we have scarcely admit of misinterpretation. When the post-abdomen first becomes free from the parent zooid, the ovary contained in it has a large number of ovarian ova in various stages of growth. That some of these mature, become fertilized, and develop into tadpoles is proved by direct observation. When the full tadpole stage is reached, only a very limited number of individuals—ten to sixteen—is present in each cavity, and the cavities contain nothing else than the tadpoles. The ovarian ova are distinctly amoeboid in form and certainly contain ingested cells. The conclusion seems inevitable that by far the larger portion of the ova of each ovary are consumed as food by the few of the same ovary that develop into embryos; furthermore, that the granular material (food yolk) of the parental mesenchyme cells is also made use of as food by the growing embryo, and that probably other tissues of the parent zooid are used, to some extent at least, in the same way.

The absence of follicular epithelium and “test” cells from the ovarian ova is undoubtedly correlated with the amoeboid nature of the ova; but it is quite possible that their absence is more apparent than real. Some of the cells ingested by the ova may represent either follicular or “test” cells, or both. The observations also seem to indicate that the test, or “cellulose mantle,” of the late embryos and tadpoles engulf various portions of the parental zooids, and this suggests that the embryos are in some way nourished by this means. Such a process, however, would be quite remarkable, and further observations on the point are greatly to be desired.





## THE HOMOLOGIES OF THE OCCIPITAL AND FIRST SPINAL NERVES OF AMIA AND TELEOSTS.

EDWARD PHELPS ALLIS, JR.

IN a recent and extensive work Fürbringer (No. 2) treats of those nerves of vertebrates that lie between the vagus, or vago accessorius, and the first free spinal nerve. This last nerve, although not definitely so defined by him, is seen, by inference, to be the first nerve posterior to the last one that issues from the cranio-spinal canal either through a foramen in the cranium or by an aperture that lies anterior to a dorsal vertebral arch segmentally related to the cranium. The nerves that lie between this first free spinal one, so defined, and the vagus are all included under the general term spino-occipital, and are subdivided into two groups. The nerves that are assigned to one of these two groups are said to have belonged, with their associated skeletal elements, since an early phylogenetic period, to the occipital region of the skull, and they are accordingly called the occipital nerves. Those belonging to the other group are said to have acquired their relations to the cranium by a more recent assimilation of their associated skeletal elements, and to be as yet but incompletely emancipated from the spinal nerves. As they thus represent an intermediate stage between the nerves of the first group and the free spinal ones they are called the spino-occipital nerves. These three names for the nerves here under consideration will be adhered to in the present article, although I think the adoption of them in the present state of our knowledge of the subject a needless complication, and even a possible source of error or inconvenience.

From Fürbringer's several special descriptions of these two groups of nerves, and his several general statements regarding them and their associated skeletal elements, it is seen that he considers as occipital nerves all those that issue from the

cranium in that part of it that lies between the posterior limit of the protometameric cranium of Sagemehl's descriptions (No. 6, p. 526) and the posterior limit of the paleocranium; and that he considers as spino-occipital nerves all those that issue in that part of the auximetameric skull of Sagemehl's descriptions that lies posterior to its protometameric portion.

These definitions of these nerves seem at first sight to be morphologically concise and definite. A little consideration will, however, show that two suppositions can be made regarding the segmental position of the nerves thus incorporated in the skull. They can either lie, morphologically, between the dorsal arches of two adjacent assimilated vertebrae, and so become enclosed between those vertebrae as they fuse with each other and with the skull; or they can lie, morphologically, posterior to the dorsal arches of the assimilated vertebrae, become first incorporated in those vertebrae and then with them in the skull. Under the first supposition the last nerve incorporated in the skull would lie anterior to the dorsal arch of the last incorporated vertebra, and anterior to the intermuscular septum related to that vertebra. Under the second supposition it would lie posterior to the same arch and septum. Each nerve of the series would accordingly belong, under the first supposition, to a trunk muscle-segment one anterior to the one it would belong to under the second supposition. From Fürbringer's descriptions it is not evident, in each particular case, to which of these two categories the nerves under consideration belong. That, in ganoids and teleosts at least, he considers them as belonging definitely to the first category is evident from his statement regarding *Polyodon*. Of this fish he says (No. 2, p. 449): "Für mich bildete das Verhalten an dem untersuchten Exemplare von *Polyodon*, wo die erste dorsale Wurzel (a) eine durch ein partielles Ligament markierte Stelle des Schädels passirt, das entscheidende Kriterium. In dieser Stelle erblickte ich die noch nicht vollkommen verwischte Grenze zwischen dem selachierartigen (protometameren) Cranium und der Wirbelsäule, und in der dorsalen Wurzel diejenige des ursprünglichen ersten Spinalnerven, der nun zum ersten occipito-spinalen Nerven (a) geworden ist."

It is thus evident, in so far at least as the ganoids and teleosts are concerned, that the most anterior spino-occipital nerve of Fürbringer's nomenclature must lie, morphologically, between the protometameric part of the cranium and the first posterior assimilated, or partly assimilated, vertebra. The most posterior spino-occipital nerve, where there are more than one, should then lie, necessarily, between the last and the next to the last assimilated vertebrae, and the first free spinal nerve between the last assimilated vertebra and the first free one. These necessary relations of the last-named nerves to the skull and vertebrae, thus definitely indicated by inference, seem not to have been carefully borne in mind by Fürbringer in his general definitions and conclusions, although it is sufficiently evident that they are of primary importance in any attempt at comparison.

In *Amia calva*, Fürbringer found, as I had found independently of him (No. 1), four nerves between the vagus and the first free spinal nerve. The most anterior of these four nerves is said by him to belong to the occipital nerves of his nomenclature, the other three to the spino-occipital ones. The occipital nerve is designated by the letter *z*, the other three by the letters *a*, *b*, and *c*. The nerve next posterior to the nerve *c* is said to be the first free spinal one, and is designated by the number 4. In other fishes, in which there may be other occipital or spino-occipital nerves, not found in *Amia*, the additional occipital ones are said to always lie anterior to the one occipital nerve of *Amia*, and the additional spino-occipital ones always posterior to the three spino-occipital ones of that fish.

In teleosts, Fürbringer finds but two spino-occipital nerves, and he considers them as the homologues of the nerves *b* and *c* of *Amia*. On page 465 of his memoir he says, that the occipital nerves are wholly wanting in all teleosts, and that the existence of the first spino-occipital one has not yet been established in any teleost known to him. On page 543 he further says, that in teleosts, not only all the occipital nerves but also the first spino-occipital nerve is "vollständig rückgebildet." The nerve next following the nerve *c* is said to always be, as in *Amia*, a free spinal one, and it is accordingly designated, as in that fish, by the number 4.

In my work on *Amia*, already referred to, I fully described all the occipital and first free spinal nerves in that fish, giving at the same time their relations to the anterior muscle-segments of the trunk, and the relations of these segments and their myosepta to the bones of the skull, to the anterior vertebrae, and to the bones of the shoulder girdle. Similar descriptions of these nerves, and of the segments and bones they are related to, form part of a work I have now nearly finished on *Scomber scomber*. The dissections of this fish have been made under my direction, in my laboratory here at Menton, by Dr. J. Dewitz, and can be briefly summarized as follows :

The sixth intermuscular septum is the first one that extends from the mid-dorsal to the mid-ventral line of the body. The ventral parts of the fifth and fourth septa, as seen on the inner surface of the body wall, run downward, from the vertebral column, on to the dorsal edge of a large accessory shoulder-girdle bone, and there end. On the outer surface of the body the fifth septum runs downward and forward to the hind edge of the clavicle, at about the middle of its length, and there ends. The fourth and more anterior septa run downward to and end at the dorsal edge of the same bone. The sixth muscle-segment, the one that lies immediately in front of the sixth septum, is thus the first one that extends ventrally the full length of the clavicle, and the fifth septum is the one that marks the apparent septal position of the ventral end of the clavicle. The fifth septum of *Scomber* is thus, in its relation to the clavicle, the apparent homologue of the same septum in *Amia*.

Centrally the fifth septum is attached to the second free vertebra of the fish, the fourth septum being attached to the first vertebra. Articulating with each of these two vertebrae there is, on each side, a single rib, which lies in the intermuscular septum attached to the vertebra, at the line where that septum is intersected by the horizontal muscle-septum. On the third and next following vertebrae there are, in addition to these horizontal ribs, ventral ones, which lie along the inner surface of the trunk muscles, in the mesial edges of the septa of the vertebra to which they are related. In one specimen a short rudimentary ventral rib was found on the second vertebra also.



The second and third intermuscular septa have their central attachments on the occipital part of the skull, the large occipito-suprclavicular ligament lying in the third septum, with its outer end in the horizontal line of the outer ends of the horizontal ribs.

The line of attachment of the first septum traverses the hind end of the posterior process of the intercalar, and the pedicle and three other processes of the suprascapular are enveloped in, or lie in definite relations to, different parts of it.

The anterior muscle-segments, on each side of the head, extend forward on the dorsal surface of the skull in two deep grooves, the lateral one of which corresponds closely in position to the temporal groove of *Amia*. This groove lies, however, in *Scomber*, on the dorsal surface of the parietal and frontal bones instead of, as in *Amia*, between those bones and the chondrocranium. The anterior margin of the muscle-segments in *Scomber* extends forward slightly beyond the posterior portion of the supraorbital lateral canal, covering externally that canal, while in *Amia* it only reaches, approximately, the hind edge of the frontal bone. The temporal extensions of the trunk muscles, which are certainly secondary adaptations, thus extend considerably farther forward in *Scomber* than they do in *Amia*.

In *Amia* the first intermuscular septum has the same general relations to the intercalar and to the pedicle of the suprascapular that the first septum in *Scomber* has. The fourth and fifth septa have their central attachments to the two occipital arches, and each usually contains one of the two occipito-suprclavicular ligaments of the fish. In one larval fish these two ligaments were found in the third and fourth septa.

In *Scomber* the dorsal and ventral roots of the nerves of the fifth and sixth trunk-segments both traverse foramina that perforate, respectively, the first and second free vertebrae of the fish, the foramina in each vertebra lying posterior to the intermuscular septum that has its attachment to the vertebra. Both nerves have dorsal, ventral, and horizontal branches, and from each nerve a communicating branch is sent dorsally, but

morphologically forward to the dorsal branch of the next anterior nerve.

The ventral branch of the nerve of the fifth segment sends a large branch forward to join a nerve formed by the fusion of the nerves of the three next anterior segments. From the large nervous trunk, so formed, a branch is sent downward and forward to the sternohyoideus muscle, the remainder of the trunk, as the *nervus pterygialis*, continuing downward and backward to the pectoral fin. After giving off this anterior branch, the main nerve continues downward and enters the ventral fin, no other branch being sent from it to the pectoral fin.

The ventral branch of the nerve of the sixth segment sends an important branch forward to join the nerve of the fifth segment, the branch joining the latter nerve distal to the point where the anterior branch of that nerve is sent forward to join the three next anterior nerves. As this branch thus forms part of a plexus which is evidently the so-called brachial plexus of the fish, it is highly probable that the nerve of the sixth segment takes part in the innervation of the pectoral fin. After giving off this branch the main nerve continues downward and enters the ventral fin.

The nerve of the seventh segment has no perceptible connection with the anterior nerves. It thus, in all probability, takes no part in the formation of the brachial plexus, and consequently no part in the innervation of the pectoral fin.

Anterior to the nerve of the fifth muscle-segment, between it and the vagus, there are in *Scomber* but three nerves. The two posterior ones are represented by both dorsal and ventral roots; the anterior one by a ventral root only. All of these roots traverse foramina in the *occipitale laterale*, the foramina lying close together and varying in number from two to five. The one or two foramina of the posterior nerve were always found separate and distinct from those of the two anterior ones, and they lay posterior to, and close to, the third intermuscular septum. Whether the foramina of the two anterior nerves also lay posterior to this septum, or were traversed by it, or lay anterior to it, was not noted. The five roots issue close

together, and the common ganglionic mass formed on them lay always posterior to the septum.

From this ganglion three dorsal, three ventral, and two horizontal branches arise, but as the anterior one of the two latter branches soon separates into two nearly equal parts, there are thus three horizontal branches, in all, associated with the ganglion. The three dorsal and three horizontal branches are distributed to the fourth, third, and second muscle-segments, in a manner similar to that of the corresponding branches in the posterior segments. The three ventral branches unite to form a single nerve which, after being joined by a branch of the nerve of the fifth segment, is distributed, as above stated, to the sternohyoideus muscle and to the muscles of the pectoral fin. As the branches of these three segmental nerves all arise from a single ganglion, there were naturally no anterior communicating branches associated with them.

There was no indication whatever of a separate nerve related to the first muscle-segment, and no branches of the nerve of the second segment could be traced forward into it.

In *Amia*, the four spino-occipital nerves belong to the second, third, fourth, and fifth muscle-segments, there being in *Amia*, as in *Scomber*, no separate nerve related to the first segment. The nerves of the second and third segments issue from the cranium through foramina in the occipitale laterale, the next two issuing through apertures in the membranes that fill the spaces between the cranium and the occipital arches. The first two nerves are represented by ventral roots only, the other two by both dorsal and ventral roots. All four of the nerves take part, as do the nerves of the corresponding segments in *Scomber*, in the innervation of the sternohyoideus muscle, and a part of the fourth nerve joins the nerve of the sixth muscle-segment to form the nervus pterygialis. Posterior to the nerve of the sixth segment several other nerves enter, independently, the pectoral fin.

We thus see that the first six muscle-segments of the trunk of *Scomber* closely agree, in their relations to the dermal bones of the cranium and shoulder girdle, with the corresponding

segments of *Amia*; and that the nerves related to these segments in the two fishes, that is, the first five postvagal nerves, agree even more closely with each other in their general peripheral distribution. The relations of these several nerves and segments to the skull and vertebrae are, on the contrary, totally different in the two fishes; for the fourth and fifth intermuscular septa have their respective attachments, in *Scomber*, to the first and second free vertebrae, while in *Amia* they have their attachments to the two occipital arches. This marked difference in the two fishes would find an evident and simple explanation in the assumption that the first two free vertebrae of *Scomber* were, in *Amia*, partly incorporated in the occipital part of the skull. But this assumption is directly opposed to Fürbringer's general conclusions, according to which it must be assumed that the first two free vertebrae in the two fishes are strictly homologous. Under the first assumption there would be, in the two fishes, a marked accord in the nerves and muscle-segments of the region. Under the second assumption there are marked differences to be explained and accounted for.

In *Scomber*, for instance, the fourth muscle-segment lies between the hind end of the skull and the first free vertebra, and it is innervated by the posterior one of the three nerves that issue through the foramina in the occipitale laterale. The next, or fifth, muscle-segment lies between the first and second vertebrae, and is innervated by the first free spinal nerve, the roots of that nerve traversing foramina that lie in the first vertebra close to, but posterior to, the intermuscular septum that has its attachment to that vertebra. In *Amia* the first free spinal nerve innervates the muscle-segment that lies between the hind end of the skull and the first free vertebra. The homologue, in *Scomber*, of the first free spinal nerve of *Amia* is, accordingly, in so far as the morphological relations of the nerves to the skull and vertebrae are concerned, the last spino-occipital nerve, and not the first free spinal one. The insufficiency of Fürbringer's definitions is thus at once evident, for an examination of the skull alone in the two fishes would not in any way indicate that the last spino-occipital nerve was not, in each, similarly related to the last occipital vertebra.



But even if this difference in the morphological relations of the nerves to the vertebrae were evident in the skull alone, Scomber would still present a marked exception to Fürbringer's general formula ; for, if the most anterior spino-occipital nerve of this fish is considered as nerve *b* of his nomenclature, the most posterior one would necessarily be nerve *d*, and not nerve 4 ; and such a nerve is not given, or its existence intimated, in any of the teleosts considered by him. If, on the contrary, the most posterior nerve is to be considered as nerve *c*, the most anterior one would be nerve *a* ; a nerve said by him to be absolutely wanting in all teleosts.

The successive incorporation of vertebrae in the occipital part of the skull is attributed by Fürbringer, primarily (unmittelbar), to the reduction and disappearance of the myomeres that give to the vertebrae in question their movements relative to each other and to the skull (No. 2, p. 548). This same reduction and subsequent disappearance of the anterior muscle-segments is also said to precede and be the primary cause of the reduction and disappearance of the nerves related to them (No. 2, p. 543).

Why, then, is there, in the adult of both Scomber and Amia, an anterior muscle-segment, relatively well developed, without any indication whatever of a separate spinal-like nerve related to it? And why is it that in Amia the last so-called occipital vertebra is incorporated in the skull after the fish has passed the age represented by a 50 mm. specimen, and yet, between the age represented by a 12 mm. larva and the adult fish, there is no related reduction in the number of myotomes? As there are, both in the adult and in larva, four muscle-segments anterior to the one that, in the adult, lies between the last assimilated vertebra and the next anterior one, some reduction in this number might have naturally been expected. In *Acipenser ruthenus*, according to Sewertzoff (No. 7, p. 232), there are always, in the adult, two or three spino-occipital nerves anterior to the one that innervates the most anterior myotome.

The temporal extensions of the trunk muscles certainly represent to some extent, in Scomber and in Amia, independent invasions of the cranial region, for in Amia these muscles lie

internal to the parietal bone, while in *Scomber* they lie external both to that bone and to the frontal. This seems to indicate that *Amia* and *Scomber* represent separate lines of descent from some fish in which the trunk muscles had not as yet invaded the temporal part of the skull to the extent they have in these two fishes. In *Scomber*, the muscles extend farther forward than they do in *Amia*. If, then, there are in *Scomber* two less anterior myomeres than there are in *Amia*, and the anterior segments in both fishes are in process of reduction, what is the explanation of this independent and apparently aggressive activity in the muscles?

Furthermore, aside from the fact that the last spino-occipital nerve perforates the occipitale laterale, I find no indication whatever, in the skull of *Scomber*, of the incorporation in it of either of the two occipital vertebrae of *Amia*; and the simple fact that this nerve is incorporated in the occipital part of the skull is not necessarily any indication whatever, in any fish, of its being a spino-occipital rather than a post-occipital one.

My work thus leads me to conclude, not only that the spino-occipital and first free spinal nerves in *Scomber* and *Amia* are homologous structures, but also that the first two free vertebrae of *Scomber* are represented in *Amia* by the two incompletely incorporated occipital vertebrae. In this my conclusions are directly opposed to those arrived at by both Sagemehl and Fürbringer in their comparisons of *Amia* with other teleosts.

Sewertzoff (No. 7, p. 240), in his examination of the skull of *Amia*, simply confirms Sagemehl's earlier observations; that is, he finds three spino-occipital nerves instead of four. In *Lepidosteus osseus*, he says (No. 7, p. 238) that Balfour and Parker's investigations show that the myotomes in embryos of that fish extend forward to the ear capsule, exactly as his own investigations show that they do in embryos of *Acipenser ruthenus*. In the adult *Lepidosteus*, he finds on each side of the head, in addition to the two foramina said to have been previously described by Gegenbaur, a third and more posterior one which "durch eine enge Ritze, wie durch einen Riss mit dem hinteren Rande des Bogens verbunden ist" (No. 7, p. 239). The anterior of these three foramina perforates the occipitale

laterale, the other two the "angewachsenen" occipital arch of the fish. The posterior foramen is said to resemble exactly the foramina found in the dorsal arches of the free vertebrae, and Sewertzoff hence concludes that it unquestionably gives passage to a spinal-like nerve. This nerve is said by him to "belong" to the so-called occipital arch of the fish and to indicate, with the next anterior nerve, that that arch is formed by the fusion of two dorsal vertebral arches instead of representing but one such arch, as Gegenbaur asserts. The drawing which accompanies Sewertzoff's descriptions seems to me to show, beyond question, that the nerve here under consideration, and the following spinal ones, each innervate the muscle-segment that lies immediately posterior to the arch the nerve in question perforates. The last nerve that perforates the skull is, accordingly, a post-occipital and not a spino-occipital one, exactly as in Scomber; and as it seems, both from Sewertzoff's figure and descriptions, to have been but recently, and still incompletely, incorporated in the skull, this may account for its apparent absence in the specimen described by Gegenbaur. This nerve in *Lepidosteus* is considered by Sewertzoff as the homologue of the last spino-occipital nerve in *Amia*; and the two vertebral arches said to be represented in the single occipital arch of *Lepidosteus* are accordingly considered as the homologues of the two partly assimilated occipital arches of *Amia*. If the posterior spino-occipital nerve of *Lepidosteus* is, as it seems to be, a post-occipital nerve, this comparison is evidently not correct.

With *Acipenser*, so fully described by Sewertzoff, I am unable to make any comparison, the embryos of *Amia* that I have as yet investigated not having been sufficiently young to show whether or not a certain number of the anterior postotic somites disappear in this fish without giving origin to permanent muscle-segments. It seems to me, moreover, that there is some confusion in Sewertzoff's descriptions. On pages 224-8 of his memoir he says, that in stage *B* of *Acipenser* the first myotome posterior to the ear capsule still exists, but is relatively much reduced in size. The first dorsal root in the specimen representing this stage lay opposite the fifth myotome on the

right side of the head, but opposite the sixth myotome on the left side. The first ventral root lay opposite the fourth myotome on both sides of the head. In stage  $B_2$  the first myotome is said to still exist, and the nerves to have the same relations to the myotomes as in stage  $B$ . In stage  $C$  the reduction of the anterior myotomes is said to have advanced no further than in the preceding stages. The first two myotomes in this stage are then said to have no related nerves, the third and fourth to have ventral roots related to them, and the fifth to have a complete spinal nerve. Later he says of this same stage, "verschwunden sind das vordere Myotom ( $M_1$ ) des Stadiums  $B_2$  und die vordere ventrale Wurzel ( $sp.d_1$ )" and "jetzt ist das vordere Paar der dorsalen Wurzeln, (welches gegenüber den Myotomen des 6ten Paares,  $sp.d_2$ , Fig. 1, lag), von beiden Seiten gleich entwickelt." That he has here in some way changed the numbering of the myotome seems evident, but it is, nevertheless, not at all certain, for although he says in one place that the number of myotomes has changed, he says in another that it has not changed. Whether this uncertainty in the numbering is perpetuated or not in the descriptions of later stages is difficult to judge. So far as the adult is concerned, the definite statement on page 232, that there are no myotomes anterior to the post-occipital one, shows a condition totally different from that found in *Amia*. The post-occipital myotome is said to be innervated, as it is in *Amia*, by the first free spinal nerve.

In the Characinidae, Sagemehl (No. 5, p. 58) found but one spino-occipital nerve, and he considered it as the homologue of the middle one of the three spino-occipital nerves found by him in *Amia*; that is, as the homologue of nerve  $b$  of Fürbringer's nomenclature. The first nerve posterior to this nerve is said to lie posterior to the stapes, and to innervate the muscle-segment that lies between the first and second vertebrae. The stapes is said to represent the dorsal arch of the first vertebrae, and the claustrum to be the homologue of the posterior occipital arch of *Amia*. As the nerve  $b$  in *Amia* lies anterior to the anterior occipital arch of that fish, there are thus, according to Sagemehl, two nerves missing in the Characinidae, one of which would be the homologue of the nerve  $c$  of *Amia*,



and the other the homologue of the post-occipital or first free spinal nerve. The latter nerve, although wanting in the Characinidae, is said to be found in *Silurus glanis*, and to lie in that fish between the claustrum and stapes.

There are thus, according to Sagemehl's descriptions, exactly the same number of spinal, or spinal-like, nerves indicated in the occipital part of the skull of the Characinidae as are found in *Scomber*, and they have exactly the same relations to the vertebral components of the skull. The same is true, according to his descriptions (No. 5, pp. 527, 543), of many other teleosts, among which may be mentioned *Esox*, *Umbra*, *Perca*, the *Gadidae*, *Cyprinodontidae*, and *Cyprinidae*. In the *Cyprinidae* the nerve *c* is said to be wanting, as it is in the Characinidae. In the other fishes named, excepting *Esox*, it is said to be found. Whether it is or is not found in *Esox* is not stated. Fürbringer, however, gives it in this fish (No. 2, p. 466). In the Characinidae, Fürbringer gives nerve 4, differing in this from Sagemehl. He agrees with the latter author as to the absence in these fishes of nerve *c*. My work would incline me to think that the nerve considered by both these authors as nerve *b* was in reality nerve *c*, and that nerve *b* had been missed by both of them in dissection.

In Carassius, Sewertzoff says (No. 8, p. 423) there are three dorsal vertebral arches in the occipital part of the skull. In *Amia* I found (No. 1, p. 727) that the same number of arches were indicated in the region occupied by the cartilaginous occipitale laterale, and that this number of vertebral arches corresponded to the number of muscle-segments. The muscle-segments in *Scomber* indicate a similar number of vertebral arches in the occipital part of the skull of that fish, *Scomber* thus agreeing in this with *Carassius*.

In *Salmo salar*, Harrison (No. 3) gives two persistent occipital muscle-segments, and says that a third and more anterior segment, found in embryos twenty-four days old, disappears entirely after that age. The first persistent segment is said to have no spino-occipital nerve related to it. The second segment is said to be related to the hypoglossus, which nerve in young stages is found "von demselben Bau als die übrigen" spinal

nerves, but in older ones is usually represented by a ventral root only. The third segment lies between the hind end of the skull and the first free vertebra, and the nerve related to it is said to be the first spinal nerve. This nerve, however, leaves the vertebral canal with the hypoglossus, "durch eine einzige Oeffnung zwischen dem Occipitale und dem ersten Wirbel." What this opening may be in or through is not indicated, but the fact that the hypoglossus traverses it warrants the supposition that, in the adult, it must be enclosed in the hind end of the skull. The post-occipital nerve of *Salmo* thus probably agrees, in this respect, with the corresponding nerve in *Scomber*. Young larvae of *Salmo* also agree with *Scomber* in the number of occipital muscle-segments, but there is, in *Salmo*, one less spino-occipital nerve than in *Scomber*.

In *Necturus*, Platt (No. 4) says that the first postotic somite aborts and disappears without giving rise to muscle fibers, and that this is true also for all other vertebrates above the *Selachii* of which she knows. If it be assumed that *Amia* agrees in this with *Necturus*, the nerve of the fifth muscle-segment is seen to be, in both these animals, the anterior nerve of the brachial plexus. The dorsal arch next posterior to this nerve is, in *Amia*, the posterior occipital arch. In *Necturus* it is the arch of the third free vertebra. The skull of *Amia* would thus, under this assumption, contain three vertebrae found free in *Necturus*. If, on the contrary, it be assumed that the first postotic somite of *Amia* does not disappear, but gives origin to muscle fibers, the two occipital arches of *Amia* would correspond to the dorsal arches of the first two free vertebrae of *Necturus*, as they do to the dorsal arches of the same vertebrae in *Scomber*. The occipital arch of *Necturus* would then represent the entire cartilaginous occipitale laterale of *Amia*, if that structure represents but a single vertebral element, or the posterior one of the three vertebral elements that enter into it, if there are three. Which of these two suppositions, if either, is the correct one can only be known after the investigation of larval stages of *Amia* earlier than any I have as yet examined.

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# ZOÖLOGICAL BULLETIN.

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## NOTES ON THE FINER STRUCTURE OF THE NERVOUS SYSTEM OF *CYNTHIA* *PARTITA* (VERRILL).

GEORGE WILLIAM HUNTER, JR.

IN the fall of 1897, while working upon the morphology and finer structure of the nervous system of *Cynthia partita* (Verrill), after noting the papers of Von Lenhosseck ('95), Dehler ('95), McClure ('96), and Miss Lewis ('96), I was led to look for the centrosome and sphere in the cells of the central nervous system. I was directly prompted to this investigation by an examination of the plates of Van Beneden and Julin's ('84) early paper on the central nervous system of the Ascidians. In Pl. I, Figs. 2 and 3, these authors represent ganglion cells with excentric invaginated nuclei. Careful study showed the same thing to be true for the ganglion cells of *Cynthia*. I was, however, not immediately successful in staining the centrosome, although later material killed in more favorable reagents showed that a structure homologous with the centrosome and sphere of authors exists in the tunicate ganglion cell. The incomplete notes on fibrillar structure of the nerve trunks are given in view of the recent papers of Apathy ('97) and Bethe ('98). It is hoped in a later paper to give a more complete account of the cell structures and their relation to the neuron.

### METHODS.

Several fixing fluids were employed. They were found to be of extremely varying utility as preservatives of the finer structure of the central nervous system. The fluids of Flem-

ming, Hermann, Von Rath, and aqueous or alcoholic solutions of corrosive sublimate gave uniformly favorable results. Specimens were left in Flemming or Hermann from one to two hours, and in corrosive from one-half an hour to six hours, according to the size of the specimen. The shorter periods gave better results. The method of Von Rath was somewhat modified. Specimens were left in his picro-acetic-platinic-cosmic mixture from one to four hours, washed six hours in methyl alcohol, twenty-four hours in pyroligneous acid, and several days in weak alcohol, before leaving permanently in 95%. Such specimens, passed through xylol or oil of bergamot, imbedded in paraffin, and cut from two to three *micra* thick, gave the most satisfactory results, especially when stained in Heidenhain's iron-haematoxylin. Of the other killing fluids used I found Lang's fluid, Gilson's mixture, and Perenyi gave the most satisfactory results. Chromic, chrom-acetic, chrom-nitric, and corrosive-acetic mixtures shrink the cell-body badly, giving it a vacuolated and fibrillar appearance. Formalin (except in very weak solution), picro-formalin, and picric mixtures were of even less value, destroying the cell elements greatly. As stains, Heidenhain's iron-haematoxylin, with safranin and Biondi-Ehrlich as controls, were employed for general work. The methylen blue-eosin mixture of McClure, and cyanin and erythrosin were used to demonstrate the chromophilous substance in the nerve cell. To demonstrate the structure of the cell prolongations and nerves, thin sections were stained from two to three days in iron-haematoxylin and the stain only partly drawn out. This method gave very favorable results.

#### STRUCTURE OF THE NERVE CELL.

The cells of the so-called brain differ greatly in size, the largest being situated most peripherally, the smallest most internally. The largest ganglion cells measure 12 *micra*  $\times$  16 *micra*, and have a nucleus measuring 4 *micra*  $\times$  9 *micra*. Those of medium size, composing the greatest number of cells in the ganglion, average 7 *micra*  $\times$  14 *micra*, with nuclei measuring 3 *micra*  $\times$  6 *micra*. The smallest cells are 3 to 4 *micra* across,

and 5 to 6 *micra* in length, with nuclei measuring  $3 \times 4$  *micra*. It can be seen that the nucleus is proportionally largest in the smallest cells, therein frequently taking up a large part of the cell-body. The nuclei of the smallest cells are much richer in chromatic matter than are the nuclei of the larger cells, and may easily be confounded with the so-called neuroglia nuclei.

Under the 1-12th oil immersion (Zeiss) the cell appears to have a granulo-fibrillar structure. The granular masses, which stain with haematoxylin and basic analins, are irregular in shape and size, and look in places as if they were made up of smaller granules. They are usually found concentrated in certain regions of the cell, *i.e.*, the extreme periphery, around the nucleus, and sometimes near the center of the cell surrounding the centrosome and sphere. A regular concentric grouping of these granules was scarcely ever found. In general the larger granules are found near the periphery of the cell. They are frequently found forming a reticulum or arranged in rows. It seems probable that these coarse granules are homologous with the chromophilous substance of the vertebrate nerve cell, as well as with that substance in invertebrates (McClure, Pflüge, Lugaro, and others). This is shown by double staining with methylen blue and eosin or erythrosin. Such methods show the cell to be made up of two differently staining elements—a varying number of irregular masses which stain with methylen blue, and a ground substance finely granulo-fibrillar or homogeneous, which takes the red stain. This ground substance seems to be made up of two portions: a semi-fluid (hyloplasm) and a granulo-fibrillar part. In general the blue-staining substance may be said to be restricted to the more peripheral parts of the cell. The masses vary much in size, small granules as well as large masses being seen; the former existing nearer the center of the cell than the latter. In cells containing an excentric invaginated nucleus the area opposite the inpushing of the nuclear membrane is seen to be made up of very fine granules which stain red. In such cells the chromophilous masses were found disposed in the peripheral portion of the cell, around the nucleus.

Besides the granules first described, small groups of refractive bodies — probably pigment granules — are found in some of the cells. Vacuolated spaces are frequent, but are so much increased in size by poor preservation that I am inclined to believe them artifacts. Such spaces may be filled with the hyloplasm of Nansen, Montgomery, and others.

A fibrillar or reticular structure for the nerve cell could not be absolutely proved, although the fibers from the cell process can be followed for some distance into the cell-body. The frequent arrangement of the granular portion of the cell into a sort of network suggests a reticular framework of fibers as indicated by Cajal and Van Gehuchten in the vertebrate nerve cell, or Pflüger in invertebrates.

The nerve cell is surrounded by a thin membrane and in the large ganglion is surrounded by a capsule of fine fibers (neuroglia of authors, or connective-tissue sheath). This capsule can best be seen in cells that are somewhat shrunken.

The nucleus is irregular in contour and appears circular, ovoid, kidney-shaped, or, in extreme cases, cup-shaped. Rarely the invagination has appeared to cut the nucleus into two distinct parts. Never has the nucleus been found to occupy a central position in the cell; it is always excentric, and frequently situated in an outpocketing of the cell. In unipolar cells it is usually found at the opposite end from the cell process; but in many cases it is forced by the action of the cen-

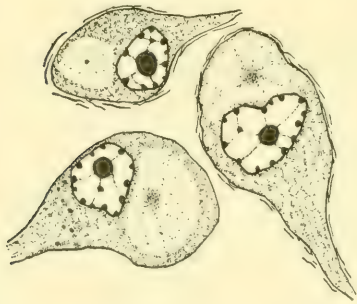


FIG. 1. — Ganglion cells. *Cynthia*. Centrosome and sphere; nucleus at axis-cylinder end of cell. Von Rath. Iron-haematoxylin. Camera drawing.  $\frac{1}{12} \times$  oc. 6 (Zeiss).

trosome close to the axis-cylinder end of the cell (see Fig. 1).

The nuclear membrane is very prominent and stains deeply with haematoxylin and basic analins. The nuclear process of Schultze ('79), Rhode ('96) was found, but it seemed to be an artifact. Binucleated cells were rarely seen.

In large cells the chromatin exists in small particles collected against the nuclear membrane and scattered through the nucleus.



These chromatin granules are held in place, as is the nucleolus, by a finely fibrous achromatic network. In large cells one nucleolus is always present, rarely two. If two are present, one is larger than the other. The nucleolus is frequently observed to be vacuolated. It is often found suspended in the achromatic network of the nucleus, but just as frequently is it found against the nuclear wall. In deeply invaginated nuclei the nucleolus is found against the nuclear wall at the bottom of the invagination, as if the wall had been pushed in until it had reached the nucleus.

In the smaller cells of old specimens as well as the cells of young animals quite a different state exists. The chromatin granules are more evident, being larger, staining deeply, and apparently more numerous than in the large cells. The nucleus, as has been noted, is much larger

comparatively than in larger cells. The nucleolus is small. There appears at first sight little difference between these nuclei and those of the so-called neuroglia cells, but a closer investigation shows the latter to be more oval and elongated and to have a less prominent nucleolus than the nerve cell (see Fig. 2). In ganglion cells of young specimens killed a few days after metamorphosis the nucleus is very rich in chromatin, and presents much the same aspect as is shown by the smaller ganglion cells of the adult specimens. The nucleus is proportionately very large, occupying the greater part of the cell-body. In the larger peripherally placed cells of the young

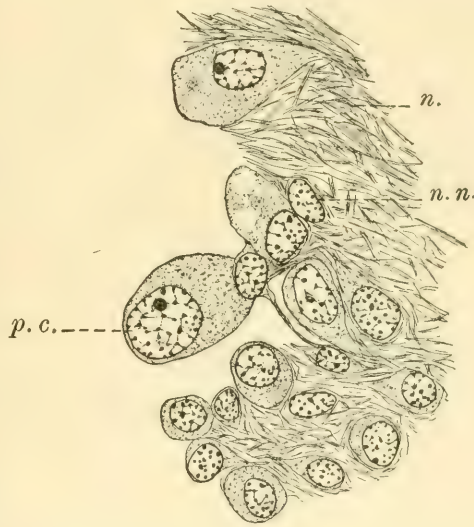


FIG. 2.—Cross-section of periphery of brain of young *Cynthia*, showing absence of connective-tissue sheath. *p. c.*, large peripheral ganglion cells; *n. n.*, neuroglia nuclei; *n.*, neuroglia and nerve fibers. Von Rath. Iron-haematoxylin.  $\frac{1}{2} \times$  oc. 6 (Zeiss).

specimens the nuclei do not occupy proportionately as much space as in the smaller cells, but still much more space than in cells of corresponding size in older specimens. The nucleus is rarely indented, usually ovoid or nearly spherical, is rich in chromatin, and contains a small nucleolus. In general the condition is more nearly that of the adult ganglion cell (Fig. 2).

#### THE CELL PROCESS AND NERVE TRUNKS.

The cell process is undoubtedly fibrillar (Schultze, Flemming, Pflüger). A decided entrance cone was frequently observed. In other cases the fibrils appeared to enter the cell-body, and spread out in the cortical part of the cell. This was especially noticeable in material killed in Flemming. In rare cases where only one large fiber or bundle of fibrils seemed to enter

the cell, it would be traced for some little distance. This may be similar to the intracellular axis cylinder of Binet ('94).

The structure of the cell process in the central system was extremely difficult to make out, but a satisfactory picture could be obtained from

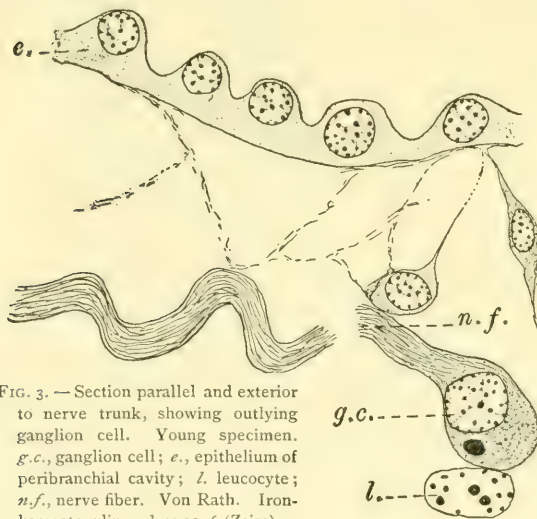


FIG. 3. — Section parallel and exterior to nerve trunk, showing outlying ganglion cell. Young specimen. *g.c.*, ganglion cell; *e.*, epithelium of peribranchial cavity; *l.* leucocyte; *n.f.*, nerve fiber. Von Rath. Iron-haematoxylin.  $\frac{1}{12} \times$  oc. 6 (Zeiss).

young specimens. In such animals the connective-tissue sheath surrounding the central ganglion is not developed, and ganglion cells are frequently found projecting into the loose connective tissue surrounding the ganglion. Indeed they are often near nerve trunks entirely free from the cell mass of the ganglion. Such a cell is shown in Fig. 3. The nerve trunk of which it is a part would be shown in the next section. The fibrillar

structure of the cell process is here plainly seen, as well as the characteristic wavy course of the fibrils. The fibrils do not form an entrance cone, but seem to spread out in the cell-body, especially toward the periphery. In the axis cylinder the fibrils appear to hold an irregular course, and do not run absolutely parallel. These fibrils are separated from each other by a homogeneous substance which does not stain with haematoxylin, and but slightly with eosin or erythrosin. This is the perifibrillar substance, probably the hyloplasm of authors. The structure of the sheath is very difficult to make out; it appears to be almost homogeneous or very finely fibrillar, as described by Apathy and Bethe. No myelin substance could be proved. In the nerve trunks the individual processes can rarely be differentiated in longitudinal section, and then only in very small, loosely constructed nerves, such as are found in the dorsal lamina. But in cross-section the structure is much easier to make out. If sections be soaked for twelve hours in the iron-alum solution, and forty-eight hours or more in the



FIG. 4. — Cross-section of nerve trunk in dorsal lamina, showing fibrils and sheaths. Adult specimen. *n.f.*, nerve fibrils; *m.c.*, muscle fibrils in cross-section. Von Rath. Haematoxylin. Camera drawing.  $\frac{1}{12} \times$  oc. 6 (Zeiss).

haematoxylin solution, then the stain is only slightly drawn out, so that the section looks black, a very good idea of the nerve trunk can be obtained. Fig. 4 shows such a specimen. The nerve trunk is usually free from any connective-tissue envelop and is found lying free in the connective-tissue space (mesenchyme). The sheath of the cell process stains a dull blue or blue black, while the fibrils take a deep black. These fibrils may be united into a little group inside the sheath (when a sheath is present) or scattered indifferently through the perifibrillar substance. Often they are found concentrically arranged just inside the sheath. Sometimes only one or two large fibrils are found.

It seems probable that one of these stages merges into

another, as Bethe holds, and not that it is an exhibition of anatomical difference between motor and sensory roots, as Apathy seems to believe. In many cases the sheath does not stain, and the fibrils appear to be loose in a non-staining perifibrillar substance. In such conditions they are usually grouped into small bundles of from two or three to a dozen fibrils. In thick sections the characteristic wavy course of the fibrils, as described by Apathy, Bethe, and others, can be seen. No heavy connective-tissue sheath is found surrounding the smaller nerve trunks. There is, however, a thin connective-tissue sheath about some of the smaller nerves, which, in the main nerve trunks, becomes quite noticeable, and forms a decided capsular sheath around the ganglion.

In the central nervous system the conditions are more difficult to make out. The structure seen could be best explained by the elementary network of Apathy or the anastomosis of Bethe. The sheath appears to be lost, and the interior of the ganglion (neuropile of authors) seems to be made up of fibers of different sizes, crossing and recrossing each other. These fibers are frequently seen to branch or divide dichotomously, but no clear cases of anastomoses have been made out. This is difficult because of the widely different courses taken by fibrils in the ganglion. Intermingled with the nerve fibrils and almost indistinguishable from them are the so-called neuroglia fibers. Neuroglia nuclei are scattered through the ganglion as well as through the nerve trunks. Whether the fibrils just described are homologous with the primitive fibrils of Apathy and Bethe, the author is not prepared to say without further research. Such, however, seems to be the case.

One interesting fact with regard to a comparison of my results with those of Nansen, who worked on the nerve tube of Ascidians (see Nansen, Pls. XXI, XXII), might be given here. It was observed that the nerve trunks, as well as the central ganglion fiber mass, when treated with chromic mixtures such as Nansen used, gave results much like those exhibited in his plates. The shrinkage caused by the chromic acid gave the nervous tissue the appearance of a number of tubes. If, however, these so-called tubes were followed to the ganglion



cells it was found that not the hollow portion of the tube but its wall seemed to make up the axis cylinder. In specimens killed in Von Rath, Hermann, Flemming, or sublimate, fluids which gave much less distortion and shrinkage, the clear area between the so-called walls of the nerve tubes is seen to be filled with fine fibrils. These fibrils in chromic material are evidently shrunken and lie close to the wall of the "tube." Indeed some specimens show the fibrils lying against the wall of the "tube."

#### CENTROSOME AND SPHERE IN THE TUNICATE GANGLION CELL.

In nerve cells containing excentric, flattened, or invaginated nuclei, as well as in many cells not showing this nuclear disturbance, were found the structures which I have taken homologous with the centrosome and sphere of Von Lenhosseck,

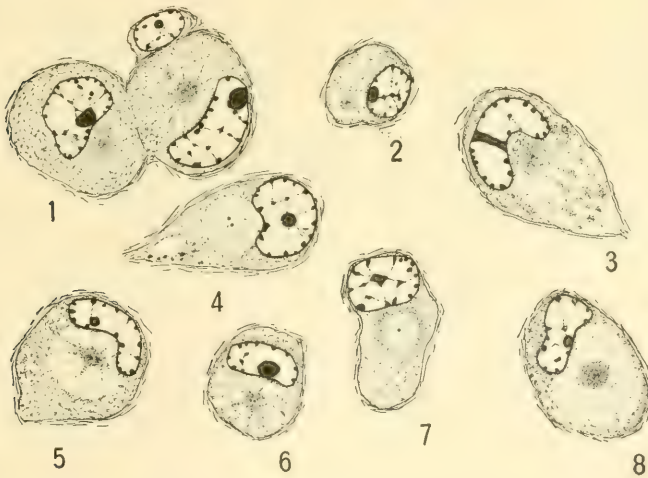


FIG. 5. —Centrosome and sphere in ganglion cells (*Cynthia*). 1, Von Rath; 2, 3, 5, 6, 8, Flemming; 4, Perenyi; 7, chrom-oxalic. Iron-haematoxylin. Camera drawings.  $\frac{1}{12} \times$  oc. 6 (Zeiss).

Dehler, Lewis, McClure, and others. In most general terms the structure can be spoken of as consisting of three parts. Beginning from the outside and going inward we have first: an outer coarsely granular zone—the granular zone of McClure and Lewis. The area of this zone varied greatly (see

Fig. 5). In some specimens it was as much as three-fourths of the cell diameter; in others it was much smaller and less pronounced. It is made up of the coarse granules of the peripheral part of the cell-body. Next is found a clearly staining area, homogeneous or finely granular, which always contains one, often several, black deep-staining granules, the centrosome or central bodies of authors. This clear area corresponds to the sphere of Von Lenhosseck or the disc of McClure. Such an area may be of considerable size and contain visible radiations which extend out into the surrounding cytoplasm (Miss Lewis), or may be reduced so as to be almost or completely wanting (see Fig. 5). The central bodies are of variable number. One large granule is frequently found; perhaps two is the most constant number. This last statement seems especially true for young cells.

The above-described type of centrosome is often met with, but there are many modifications. In some of the cells of a ganglion may be found a centrosome with well-developed astral rays, presenting the appearance found in leucocytes. In other cells of the same ganglion (see Fig. 5) may be found a centrosome with the typical archoplasmic condensation around it. In still other cells the centrosome may have little or no condensation of cytoplasm about it, and may exist as a deep-staining granule in the cell. Again, such a centrosome as last mentioned may be made up of several granules which seem to be more or less solidly welded together. All these forms or states of centrosomic activity may be present in one or the same section (see Fig. 5). This figure shows that the centrosome structure is not a fixed one, such as Von Lenhosseck pictures, but extremely variable in form, more so than Miss Lewis figures. It seems evident from this that the centrosome, as a dynamic center, is of varying importance in different cells. This is further shown by the differing amount of condensation in other cells, as well as the manner in which the nucleus is indented. In these cells, all described being from adult specimens of varying age, we see represented various-sized cells. There seems to be no restriction as to size, although the centrosome is much easier to prove in the larger cells.

It would be difficult to give the proportion of cells found which contained centrosomes, as in many specimens after staining no such structure can be proved. The nucleus, although excentric, appears ovoid or circular, and no concentric arrangement of the cytoplasm can be observed. In such cells, however, the centrosome may exist as a granule, although no such state has been proved.

Several very young animals from two to three mm. long were killed shortly after metamorphosis. In such specimens the ganglion cells, although nearly as large as in the adult, contained nuclei much larger in proportion than those contained in the adult cells. The nuclei were much richer in chromatic material than in the adult. The most striking feature noticed

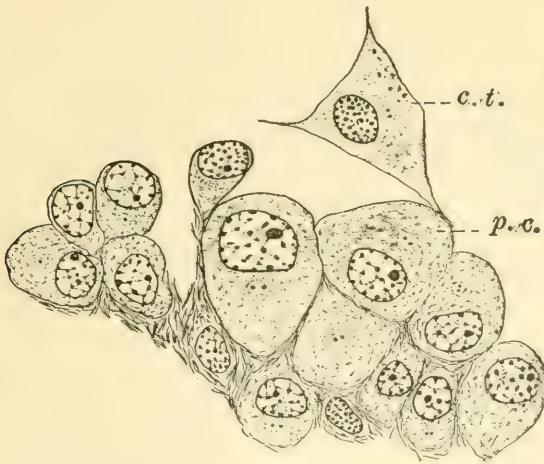


FIG. 6. — Cross-section of brain (*Cynthia*) shortly after metamorphosis, showing centrosomes in ganglion cells. *p.c.*, large peripheral cells; *c.t.*, connective-tissue cells. Von Rath. Iron-haematoxylin. Camera drawing.  $\frac{1}{2} \times$  oc. 6 (Zeiss).

was the fact that a very large proportion of the cells was found to contain centrosomes, although in most cases the sphere and radiations were lacking. It cannot be positively stated that all ganglion cells at this stage contain centrosomes, but certainly a very large proportion do, as can be seen by a glance at Fig. 6. The centrosome in these cells is usually double, *i.e.*, two central bodies are found. There seems to be no common axial relation between the direction of the two bodies and the long

axis of the cell. In general a very small clear area may be said to surround the central bodies, but it is small compared with the same area in cells of older specimens. A very slight condensation is frequently found, but it is also slight as compared with older cells. Rarely, if ever, are astral rays found. In some few cases a decided granular condensation of the archoplasmic type is found. But in the majority of cases the centrosome in the young cell differs from the same structure in the old cell, by existing without protoplasmic rays extending from the central body, frequently without any condensation of cytoplasm about it, and often exists as one or a pair of deeply staining granules, situated in the central part of the cell-body. More than all, it differs in the amount of mechanical influence exerted on the cell structures. In the cells of the young *Cynthia*, where the nucleus is proportionately so much larger than in older cells, we would expect a most decided invagination and excentricity. But such is rarely the case. Exceptionally do we find a nucleus with a decided invagination, and flattened nuclei are rare. The nucleus is, however, always excentric. It is round or ovoid in shape, rarely flattened or pushed into an outpocketing of the cell-body, as is observed in older specimens. These facts can only be explained on the supposition that the centrosome does not exert any decided mechanical influence on the cell protoplasm, as is seen by the absence of a disc, sphere, or radiations. Indeed in many small cells the centrosome seems pushed to one side by the larger nucleus.

The centrosome does not seem to have any fixed position in the cell-body. It was most frequently found between the nucleus and the cell process near the center of the cell. It was also frequently found to lie between the nucleus and that part of the cell most distant from the cell process. It might even lie laterally between the nucleus and the cell membrane. Such positions appeared to be normal.

The question of the function of the centrosome is of extreme interest, although with our present data it is very far from being solved. Von Lenhosseck has little to say with regard to its probable function, and, with Dehler, seems to consider it a centrosome once actively functioning in division but left over



in the resting cell. Miss Lewis believes the structure homologous with the centrosome and sphere in dividing cells.<sup>1</sup> McClure thinks the central bodies and disc found in *Helix* are morphologically equivalent to the centrosomes and sphere commonly found in other cells. The papers of Buhler and Schaffer I have not seen.

It is evident that, at least in certain stages of its existence, the centrosome has a mechanical influence in the cell protoplasm. As we have seen in young specimens of *Cynthia*, a condensation of cytoplasm about the central bodies, with the accompanying indentation of the nucleus, is lacking. But in such cells as contained the centrosome, with its sphere and radiations or condensation, a marked mechanical force seems to be excited. This was shown by the excentric position of the nucleus, the flattening or invagination of the nuclear membrane on the side toward the sphere, the condensation and concentric arrangement of the cytoplasm about the central body, and the frequently found radiations extending toward the periphery. However, no instances of mitotic division were found. Binucleated nerve cells were seen, and cases where nuclei were so flattened and distorted by the invagination as to be nearly divided into two parts, but in no case anything like mitosis was found. Recent investigation seems to point to the fact that nerve cells, although they may remain for a long time in a so-called embryonic state, *i.e.*, as neuroblasts functionally inactive, never divide as adult cells. No cases of mitotic division of nerve cells have been yet placed on record, so far as known to the author. It would seem, then, that another explanation must be found for the presence of the centrosome in the ganglion cell.

More recently is advanced the theory that the centrosome may be left over in the cell from its embryonic state to be called forth into activity by seasonal conditions. Such a view was hinted at by Von Lenhosseck in his reference to Meves's paper

<sup>1</sup> In Miss Lewis's second paper, "Studies on the Central and Peripheral Nervous Systems of Two Polychaete Annelids," *Proc. Amer. Acad. Arts and Sciences*, vol. xxxiii, No. 14, 1898 (which came too late to be inserted in the bibliographical list), she pictures ganglion cells containing two spheres; but she concludes that the ganglion cells, after an early embryonic period, never divide.

on the centrosome in the tendon of Achilles of the frog. Meves thinks the centrosome a permanent cell organ which in old cells may not be functionally active. Von Lenhosseck points out that Meves's observations were made on winter frogs, and thinks that perhaps with the renewal of life activities the cell might divide again. The author has not yet concluded any experiments in this direction, as his material was limited to a killing period of three months, June to September. Such experiments in *Cynthia* would be difficult, because probably no actual hibernation period takes place, although the life activities may be reduced in winter. One interesting fact might be noted, however; if the central ganglia of several specimens, killed in the same fixing fluids and exposed to same conditions of technique, are sectioned, stained in iron-haematoxylin, and examined, it is found that some specimens show nearly all the cells of the ganglia to contain centrosomes and spheres, with accompanying indentation of the nuclei, while other specimens show few if any cells in this condition, and the centrosome, if present, not surrounded with a sphere or radiations. In other words, at a given time of the year (summer), certain ganglion cells in some animals are observed to contain centrosomes, while corresponding cells in other animals seem to lack this structure. It is important to note that the age of the specimens cannot be taken into consideration, and this may be an important factor.

It seems to the writer that the centrosome in the ganglion cells must have a meaning other than cell division. Might it not serve the same function as it appears to have served in certain cells possessed of protoplasmic movement, such as leucocytes, giant cells of bone marrow, embryonic blood corpuscles, pigment cells, etc.? In leucocytes it has been shown by Flemming ('91) and Von Rath ('95) that the centrosome is apparently not engaged in mitotic division, as a sphere and central body are found existing in cells in which the nuclei are divided, seemingly by amitosis. In the liver cells of an isopod (*Porcellio*) the attractive sphere is not concerned in the division of the cell. Other like cases have been observed. In such cells as the pigment cell the centrosome appears to be a dynamic center, causing contraction or expansion (chromatophore of cephalopods).

It is well known that, in early life at least, the ganglion cell is migratory. Such a cell is shown in Fig. 3. It has wandered out from the ganglion (shown in next section), and is probably on its way to the periphery. This cell is observed to contain two centrosomes. It is worthy of note that in the mammalia the only ganglion cells in which centrosomes are found (so far as known) are those of the spinal and sympathetic ganglia. The cells of the spinal ganglia have probably migrated from the central system; the cells of the sympathetic are proved to have migrated from such a source. In the spinal cord cells bordering the central canal migrate out into the cord. These cells are the neuroblasts. The above facts seem to prove that the ganglion cell in certain stages of its existence has the power of locomotion. Might not the centrosome preside over the locomotor power of the cell—in the ganglion cell as well as in the leucocytes?

The theories of Englemann and Cajal, in regard to the movement and growth of the ultimate ends of the cell process, are interesting from this standpoint. According to these authors, the cell processes are capable of growth and may branch, forming more and more complex endings. These endings may at one time be in connection with one set of cells, at another time with another set, thus giving many new pathways between different cell groups at different times. Here again is the idea of movement of parts of the cell. Could the centrosome influence such movement? Would such movement, if it existed, be homologous or analogous to the movement in pigment cells? Such questions cannot yet be answered.

This suggestion in regard to the possible function of the centrosome in the ganglion cell must not be taken for fact or theory. It is only suggestion. Much more work must be done and many more facts gathered before such a view could be taken for a theory. But it is hoped that at some future time the problem may be successfully attacked and solved.

## SUMMARY.

The principal points treated in this paper are as follows :

I. The demonstration of the fibrillar nature of the nerve process as opposed to the "nerve tube" of Nansen. Positive proof of the elementary network of Apathy and Bethe is lacking. Such a view could, however, best explain the structure of the neuropile of the ganglion (brain) of *Cynthia*.

II. The presence in the nerve cell of ganglion bodies of different size, which color strongly with methylen blue and which are of different chemical structure from the groundwork of the cell. These bodies are undoubtedly homologous with the chromophilous substance in many invertebrates (Pflüge, McClure) as well as in vertebrates. The ground substance of the cell appears granulo-fibrillar. Frequently fibrils may be proved in the cell, especially near the process, and in the periphery of the cell. A cone of entrance was frequently found.

III. The existence of the centrosome and sphere in the ganglion cell. This structure was found in adult as well as in young specimens killed a few days after metamorphosis. In the young cell the structure more frequently existed without radiations, and with little or no cytoplasmic condensation about the central body or bodies. The centrosome was proved in a greater proportion of cells in young specimens. In older specimens the centrosome and sphere, although not limited to cells of certain size, was proved in fewer cells proportionately. When found it exhibited all possible variations from the central body with little or no cytoplasmic condensation to a decided sphere with cytoplasmic radiations extending almost to the periphery of the cell. In the latter case the nucleus was deeply invaginated and pushed far to one side of the cell, while in cells with little or no radiation and small sphere the nucleus was often ovoid, or only slightly flattened.

It is hoped in a later paper to give a more complete account of the fibrillar structure of the nerve trunks, and to throw some light, if possible, on the function of the centrosome in the ganglion cell.



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## THE MAXILLARY AND MANDIBULAR BREATH- ING VALVES OF TELEOST FISHES.

ULRIC DAHLGREN,

INSTRUCTOR IN HISTOLOGY, PRINCETON UNIVERSITY.

WHILE watching the living fishes in the aquaria<sup>1</sup> of the United States Fish Commission at Woods Holl, Mass., the writer noticed that the jaws were scarcely moved in breathing, the mouth being kept open all the time, except when used for biting or for yawning, or other acts than breathing. Further, when the fish was facing the observer and when the light was favorable a pair of large and well-developed membranous valves were seen inside the mouth, opening and shutting with a perfect automatic motion as the fish breathed.

One of these valves, which were both situated just inside of the teeth, depended from the roof of the oral cavity, while the other arose to meet it from the floor of the oral cavity just in front of the tongue. They were crescentic in shape, widest directly in front, and tapering down laterally to a point just behind the angle of the mouth. Their lines of attachment to the surfaces of the oral cavity were concentric with the teeth. In texture they were semi-transparent and extremely flexible and strong.

A few minutes' observation was sufficient to demonstrate that these structures were valves of great importance in breathing; and an examination was made of the literature on the subject.

No mention of such valves appears in the standard works on ichthyology and comparative anatomy, with the exception of Owen,<sup>1</sup> who says: "The folds of membrane behind the upper and lower jaws, of which 'internal lips' the swordfish and dory afford good examples, seem intended to prevent the reflux

<sup>1</sup> Owen, *Anatomy of Vertebrates*, vol. i, p. 413. London. 1866.

of the respiratory stream rather than the escape of food from the mouth."

Gunther<sup>1</sup> makes no mention of the organs in question, and states that "the water used by fishes for respiration is received by the mouth and by an action similar to that of swallowing is driven to the gills and expelled by the gill openings." I have found several differences between the acts of swallowing and of breathing in the teleost fishes.

Wiedersheim<sup>2</sup> states that "fishes breathe by taking in water through the mouth and, by the contraction of the latter, forcing it out again through the gill slits."

The use of the word "through" in the above quotation leads me to infer that the mouth opening is meant, and not the oral cavity.

A. B. Macallum<sup>3</sup> has mentioned these structures in his article on the "Anatomy of *Amiurus*," where he says: "Behind the pads of teeth and running concentrically with them are folds, one above and one below, arising from a relaxation of the lining membrane; that behind the maxillae is largest, but both may be absent. In one specimen of *Amiurus nigricans* the fold reached downward and backward into the cavity of the mouth fully one-half inch." No mention of the function of these folds of membrane is made.

These valves have been observed in operation by the writer in over fifty species of fresh-water and marine fishes, and no teleost has been found which does not possess them. Since no accurate description of them and of their function has become part of our recent manuals or text-books, and since, on the other hand, for want of such knowledge it has been impossible to clearly describe the act of breathing in fishes, I take this opportunity of calling attention to these valves and of demonstrating their value as organs of breathing.

These valves will first be described as they appear in the common sunfish, *Eupomotis gibbosus* (Linn.). (See Fig. 1.)

<sup>1</sup> Gunther, Introduction to Study of Fishes, p. 136. Edinburgh. 1880.

<sup>2</sup> Wiedersheim (translated by W. N. Parker), Comparative Anatomy of Vertebrates, p. 278. London. 1896.

<sup>3</sup> *Proc. of Canadian Inst.*, N.S., vol. ii, No. 3, p. 387. Toronto.



In this fish they are highly developed and efficient. The upper valve is a sheet of membrane hung from the roof of the oral cavity and covered by a continuation of its mucous membrane. Its line of attachment is slightly bow-shaped, and lies directly behind the teeth and parallel with them.

The valve is broad with a straight lower edge, in the middle of which is a thickened tooth-like projection. This projection

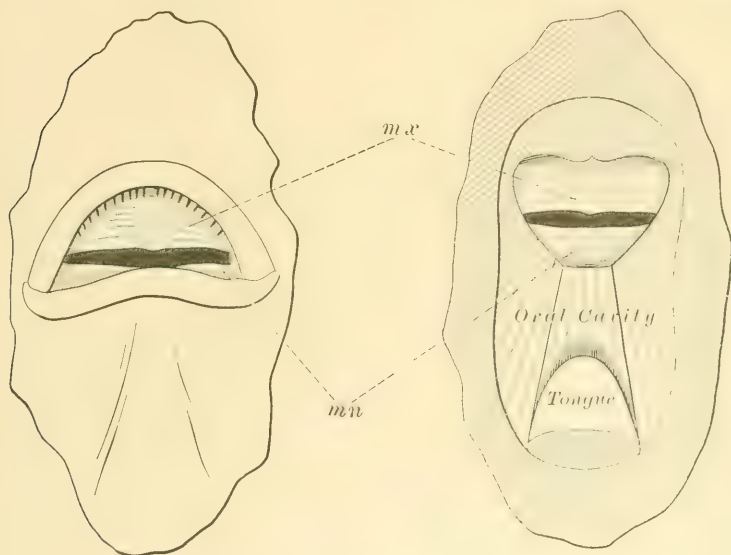


FIG. 1. — Maxillary and mandibular breathing valves of sunfish, *Eupomotis gibbosus* (Linn.). Seen from in front (A), and from behind (B). *mx.*, maxillary breathing valve; *mn.*, mandibular breathing valve.

is the lower end of a vertical median thickening of the valve. The lower valve is two-thirds as broad as the upper, and in other respects is similar to it. The median thickening is perhaps not so marked, and the valve tapers more at each lateral extremity. Sections show that each valve is a membrane of elastic connective tissue covered with a mucosa. The mucosa possesses a well-developed layer of smooth muscle, while a layer of the same kind of muscle extends from anterior surface to posterior surface at the base or line of attachment of the valve. In death the valves are found lying close to the surface of the

oral cavity with their free edges pointing backward, and if the specimen has been hardened they are more easily seen. (See Fig. 2.)

In fresh dead specimens they are very hard to detect because of their flexible texture and tapering edges, which allow them

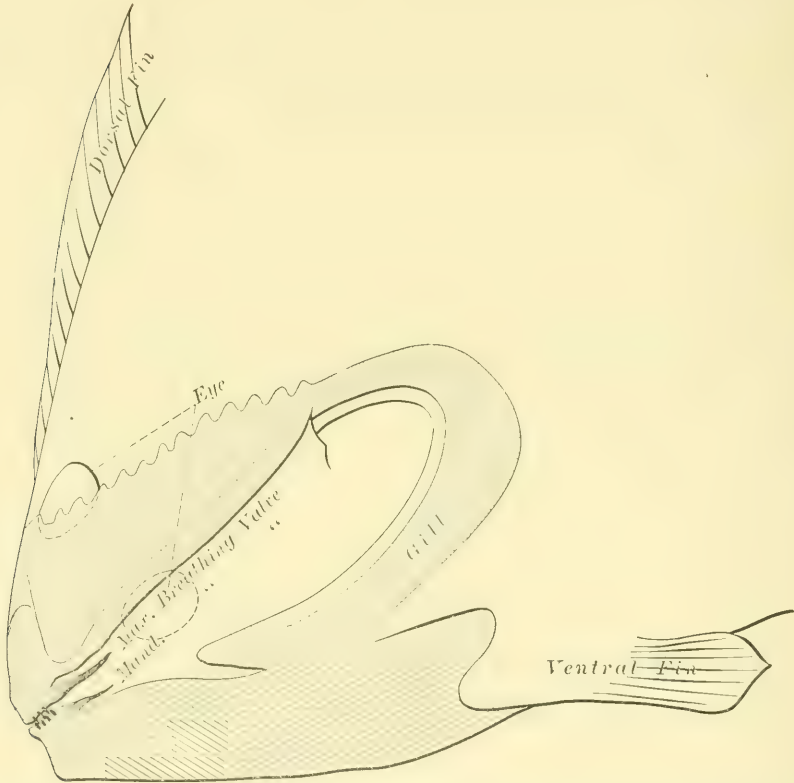


FIG. 2. — Head of flounder, *Paralichthys dentatus* (Linn.), seen from left (upper) side. The shaded area represents a vertical median section of the mouth and oral cavity to show the position of the breathing valves in an alcohol hardened specimen.

to adhere so closely to the mucous membrane of the oral cavity.

Both valves are placed with their edges pointing downward and backward at an angle of less than  $45^\circ$  to the axis of the body. This angle is increased to about  $80^\circ$  when the valves are struck by the regurgitating stream of water at the beginning of expiration.

A number of young black bass, *Micropterus salmoides* (Lac.), were carefully kept in aquaria with running water, and when they had become perfectly tame, in some weeks' time, observations were made on the rate and manner of breathing, with particular reference to the valves under consideration.

Each breath requires two acts: one of inspiration and one of expiration. During inspiration the oral cavity is enlarged by moving the opercular frames outward, thus requiring an incoming stream of water to fill the extra space produced. This stream enters the oral cavity at the mouth, which at the beginning of inspiration is open about one-fourth of its normal maximum extent. During inspiration the mouth is opened about ten per cent more, this motion being due only to the connection of the jaws with the opercular frames.

The mandibular and maxillary breathing valves are flattened back against the top and bottom of the oral cavity by the entrance of this stream of water. Meanwhile water would enter at the gill openings, which are widening, was it not for the branchiostegal membranes which, although they are attached to the opercular frames, move independently of and contrary to them, closing the entrance automatically by the action of the water that tries to enter. (See Fig. 3.)

The opposite act of expiration now takes place, the opercular frames moving inward to reduce the space in the oral cavity. The water tries to leave at the mouth, but catching on the edges of the breathing valves and then striking their posterior surfaces it forces them up into such a position that their edges meet and all further progress is stopped. The water then leaves at the gill openings.

During expiration the mouth is slightly shut, both this and its opening during inspiration being unavoidably due to the attachment of the jaws to the opercular frames, and not to an effort to retain or let out the water.

One fish of this lot was six and one-half inches long. When at rest and free from recent excitement, the number of breaths each minute was forty, with the temperature of the water at  $10\frac{3}{4}^{\circ}$  Centigrade.

This rate was very constant, and the half-yawns which the

fish occasionally gave did not disturb the rate because they also occurred at regular intervals. The fish was taken out in a scoop-net and held gently in a wet cloth while both valves were

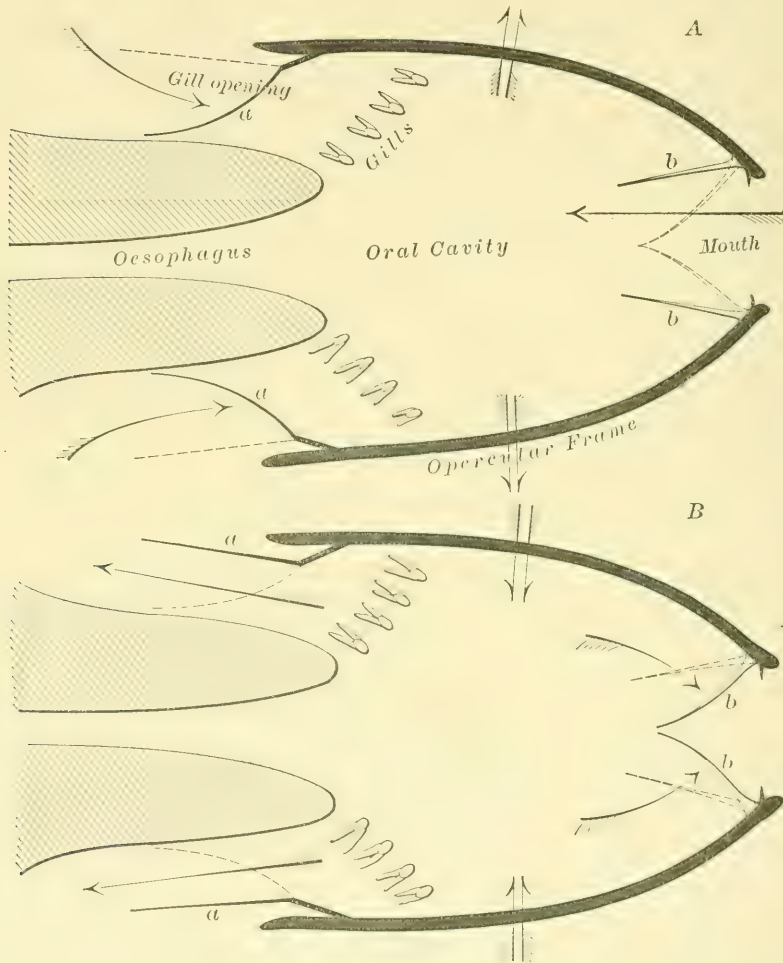


FIG. 3. — Diagrammatic representation of the pump-like structure of the teleost oral cavity. The anterior portion of each figure is represented in longitudinal vertical section, the posterior portion in longitudinal horizontal section. A, inspiration; B, expiration. Arrows represent water pressures; double arrows represent motions of opercular frames. a, branchiostegal valves; b, maxillary and mandibular breathing valves.

cut in their median line from edge to line of attachment, thus practically destroying their usefulness as valves. When returned to the water the fish darted about, but soon settled down and



in twenty minutes had apparently recovered from the effects. The rate was now fifty-nine per minute, and the manner of breathing had entirely changed. The enlargement of the oral cavity was fully a third greater than before (on a rough estimate), and at or before the beginning of expiration the mouth was tightly closed with an effort in order, apparently, to prevent the regurgitation of water. In four days this fish was breathing normally again and the valves were apparently repaired, the scar being visible on the edge as a notch, with a white line running from this notch to the line of attachment of the valve.

#### SUMMARY.

In the light of the above observations and experiments the act of breathing in the teleost fishes may be described as follows:

The respiratory stream enters the oral cavity by the mouth and leaves by the two gill openings, coming in contact with the respiratory surfaces of the gills just before it passes out. It is urged on its course by the pump-like construction and action of the oral cavity and its two sets of valves, an anterior set, which are those under consideration, and a posterior set, the branchiostegal valves.

In inspiration the stream enters at the mouth, in response to a dilation of the oral cavity produced by the outward lateral movement of the opercular frames.

At the same time water is prevented from entering at the gill openings by the branchiostegal valves which, although they are attached to the opercular frames, move independently of and contrary to them; so that, while this outward movement of the frames extends the gill openings, the branchiostegal valves close them automatically by the action of the water which tries to enter.

In expiration the water is forced out of the gill openings by a corresponding contraction of the oral cavity. At the same time the water is prevented from regurgitating through the mouth, not by the contraction of the latter, but by the automatic operation of the maxillary and mandibular breathing valves

which move as accurately and efficiently as any of the heart's valves. Caught on their posterior edges by the first movement of regurgitation, they snap together and completely prevent any water from leaving the oral cavity by the mouth which, meanwhile, is left partly open, almost as much open as during inspiration.

That these valves are of value as breathing organs is evident upon casual observation; that they are of much importance is shown by the compensatory action brought about by injury; that they are not of immediate vital importance is proved by the fish's ability to get along without their services until they are repaired.

## THE EFFECT OF TEMPERATURE ON THE REGENERATION OF HYDRA.

FLORENCE PEBBLES.

It has been shown that temperature has a marked effect on the regeneration of *Planaria torva*. Lillie and Knowlton (2) have proved by experiment that the optimum temperature at which regeneration is completed is  $29^{\circ}.7$  C.; the minimum, about  $3^{\circ}$  C.

During the last month I have made a series of experiments on *Hydra viridis* and *Hydra grisea*, in order to test the effect of temperature on the regeneration of the hypostome and tentacles. A transverse cut was made through the reproductive zone of the polyp just posterior to the ring of tentacles. The body thus deprived of hypostome and tentacles was subjected to a gradual rise of temperature. The dishes in which the *Hydras* were placed after the operation were partially submerged in a water bath in which the temperature varied from  $26^{\circ}$  to  $32^{\circ}$  C. Readings were taken during the day at intervals of four to six hours; the variation was never greater than five degrees. Control experiments were made at room temperature, which ranged between  $18^{\circ}$  and  $24^{\circ}$  C. Observations were made at intervals of twelve to twenty-four hours, and regeneration was considered complete when the new hypostome and tentacles had attained their normal size.

Normal *Hydras* were also placed in the water bath, in order to determine what degree of warmth the uninjured polyps could endure without apparent disturbance. In one series of experiments the temperature was raised to  $38^{\circ}$  C., and as a result not only the injured, but the normal, polyps died. At the end of several hours they had completely disintegrated.

That the rise of temperature up to  $32^{\circ}$  C. produces a marked decrease in the time required for regenerating the lost parts is seen in the following tables. In Table 1 the range of temperature and the percentage regenerated at a given time are

recorded. Forty-six individuals were used in a series of six experiments.

TABLE 1.—HYDRA VIRIDIS.

TEMPERATURE.	PER CENT REGENERATED.	
	48 hrs.	72 hrs.
26-27°	100%	100%
27-30°	97%	100%
28-30°	88.9%	88.9% (1 dead)

The rate of regeneration in Table 1 may be compared with the rate for *Hydra viridis* at room temperature, given in Table 2, where the results from forty-five individuals in eight experiments are given.

TABLE 2.—HYDRA VIRIDIS.

TEMPERATURE.	PER CENT REGENERATED.	
	48 hrs.	72 hrs.
18-24°	37.8%	100%

It is readily seen that the number completely regenerated at room temperature in forty-eight hours is much smaller than under higher temperature.

In a recent paper (3) I noted that the rate of regeneration of *Hydra viridis* is much more rapid than that of *Hydra grisea*. In connection with this it is interesting to find that when the temperature is raised there is a larger reduction in the time required for regeneration in *Hydra grisea* than in *Hydra viridis*. Table 3 is the record of twenty-eight individuals in five experiments.

TABLE 3.—HYDRA GRISEA.

TEMPERATURE.	PER CENT REGENERATED.	
	48 hrs.	72 hrs.
26-27°	80%	100%
27-32°	70%	100%



At room temperature, *i.e.*, 18–24° C., the regeneration is much slower. In five experiments, in which nineteen polyps were injured, there was no regeneration completed at forty-eight hours; and at the end of seventy-two hours a very small number were complete, as Table 4 shows.

TABLE 4.—HYDRA GRISEA.

TEMPERATURE.	PER CENT REGENERATED.		
	48 hrs.	72 hrs.	96 hrs.
18–24°	0%	26.3%	94.7%

In order to show the great difference in the rate of regeneration of the two species and the effect of the higher temperature, a record, in which several sets of experiments are combined, is given in Table 5.

TABLE 5.—COMPARISON OF *H. GRISEA* AND *H. VIRIDIS*.

TEMPERATURE.	PER CENT REGENERATED.		
	48 hrs.	72 hrs.	96 hrs.
<i>H. grisea.</i>			
18–24°	0%	26.3%	94.7%
26–32°	75%	100%	100%
<i>H. viridis.</i>			
18–24°	37.8%	100%	
26–30°	98.5%	100%	

Owing to lack of material, I was unable to try the effect of lower temperatures on *Hydra grisea*. The results obtained from a series of five experiments on *Hydra viridis* show that when the polyps are subjected to cold, regeneration is greatly retarded. Table 6 is the record of thirty-eight individuals at a low temperature where the thermometer was kept at 12° C.

TABLE 6.—HYDRA VIRIDIS.

PER CENT REGENERATED.				
96 hrs.	120 hrs.	130 hrs.	144 hrs.	168 hrs.
13.1%	23.7%	34.2%	71%	100%

The change in appearance of the injured region was so slight from day to day that observations were less frequent than in the experiments where the temperature was higher. It will be seen from Table 6 that by a lowering of the temperature a delay of twenty-four to ninety-six hours results in the process of regeneration. On the other hand, an increase of temperature brings about an increase in rapidity of the rate of regeneration of twenty-four to forty-eight hours for *Hydra grisea*, and also a slight increase for *Hydra viridis*.

While making these experiments with temperature, I tried the effect of colored lights upon the regeneration of *Hydra*. Four colors were tested — red, blue, green, and yellow. These colors were obtained by making solutions of congo red, copper sulphate, anilin green, and potassium bichromate, respectively. These were tested with the spectroscopé and found nearly monochromatic.

A number of experiments were made and also control experiments in darkness and in diffuse daylight, but the process of regeneration was in no way influenced by any of the colors.

The experiments noted here were made in the Physiological Laboratory of Bryn Mawr College, and were directed by Dr. J. W. Warren, to whom I wish to express my thanks for suggestions and assistance.

BRYN MAWR, PA.,  
June, 1898.

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## FURTHER NOTES ON THE EGG OF ALLOLOBOPHORA FOETIDA.

KATHARINE FOOT AND ELLA CHURCH STROBELL.

### PREFACE.

IN the autumn of 1894, while I was studying living eggs from the ovaries of *Allolobophora foetida* with a Zeiss 2 mm. immer. lens., Dr. Whitman suggested that I kill the eggs under this high magnification in order to observe the effect of the fixatives. I made many attempts, but was unable to overcome the technical difficulties sufficiently to make the method of any value. The following spring I experimented with eggs from the cocoons; but found it impossible, without injury to the egg, to hold it steadily in the field while applying the fixative. This summer, by the aid of the Bausch and Lomb compressor, Miss Strobell and I have been able to get more satisfactory results, for it has been possible with this compressor to hold the eggs firmly and yet so gently that they continue to develop normally, forming the polar bodies, etc.

Ziegler's (10) classic work on the living Nematode eggs led me in the spring of 1896 to commence the study of the living (cocoon) eggs of *Allolobophora foetida*, and at that time I began a comparative study of the living and fixed cytoplasm of these eggs. It was my aim to be able to place side by side illustrations of the living cytoplasm with illustrations of the same stages killed by different fixatives, hoping by that method to support or correct my earlier interpretations.<sup>1</sup>

Since the spring of 1897 Miss Strobell has been associated with me in this work; and, as our results have been attained

<sup>1</sup> I quote the following from a paper sent to press December, 1897, and which will appear in *Journ. of Morph.*, vol. xiv, No. 3, 1898. "As I am at work on a paper which will give the results of a comparative study of the living and fixed cytoplasm in these eggs, I shall omit here any description of the living normal cytoplasm."

by our combined efforts, we unite in bearing the responsibility of their publication, — parts of the following paper being written by each of us. Owing to the difficulties of obtaining large numbers of these eggs at definite stages of development, it will require both time and patience to make a comparative study of much value. In the present paper we shall give a brief account of such of our results as we can support with photomicrographs; and I shall also give certain results obtained from a further study of the deutoplasm of these eggs, some data bearing on the formation of the vesicles between the first and second maturation spindles, and a few notes on shrinkage.

With orange-methyl green I had differentiated the following structures in the cytoplasm (6), the network and archoplasm (polar-ring substance) selected the orange, while the nucleoli, sperm-granules, centrosomes, and the large and small granules in the spindle, attraction spheres, and cytoplasm selected the methyl green. I did not suspect that many of these granules might be deutoplasmic, for at that time I was fully convinced that xylol or xylol balsam would, in all cases, dissolve out the deutoplasmic granules in a few hours. Further investigation showed me that the time required to dissolve the deutoplasmic granules is very inconstant. In some cases it will require days, again it will require as many weeks, and in a few cases they form an insoluble compound with the stain, and cannot be dissolved at all — this last being true even when the sections have been subjected to *exactly* the same technique, in the one case the deutoplasmic granules staining weakly and readily dissolving out, and in the other staining deeply and remaining insoluble. These facts led me to suspect their identity with many of the above-mentioned methyl-green granules, and I am greatly indebted to Miss Strobell for assisting me in my experiments to determine this point.

KATHARINE FOOT.

To test the surmise that some of the granules differentiated with methyl green were identical with the deutoplasmic granules, a number of eggs were submitted to the following technical tests. The eggs were killed in chromo-acetic, as this fixative



shows a definite structure of the cytoplasm and an approximately definite distribution of the granules; osmic acid was then used, not as a fixative, but as a stain which might select the deutoplasmic granules alone. After a few minutes in 1% osmic, the eggs were hardened, imbedded, sectioned, and mounted in glycerine without further staining. An examination of the sections showed the granules intensely blackened, and as they were apparently the only constituents in the cell that responded to the osmic, we have designated them osmophile granules (Photo. 12 and Text-fig. I). The nucleoli in the pronuclei, and when present throughout the cytoplasm, were not blackened by the osmic, and the centrosomes, which were occasionally visible in the unstained sections, were a brownish-yellow. With the diaphragm open, the intensely black osmophile granules are

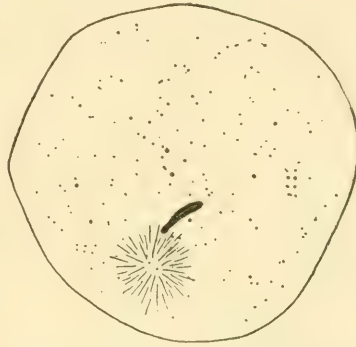


FIG. I. — Section of oöcyte, 2d order, showing one form of distribution of the osmophile granules. Osmophile granules in cytoplasm and sphere drawn with camera lucida. Rays diagrammatic.

most sharply differentiated from the centrosomes and the greenish refractive nucleoli. Photographs were taken of many of these sections, and numerous camera sketches were made, and a comparison of these with the sketches previously made of the granules that had been differentiated with methyl green (6) showed beyond question the identity of many of the latter with the osmophile granules. The above-mentioned unstained sections were then soaked in warm xylol twenty-four hours and left mounted in xylol balsam until the osmophile granules had so nearly disappeared (at first the xylol merely removes the blackening caused by the osmic) that their presence could be detected only by comparing the sections with photographs which indicated exactly where to look for each granule. The sections were then stained with orange-methyl green, and the faded osmophile granules *selected* the green and became again distinctly visible. Other sections were stained with acid fuchsin before being mounted in glycerine, and these showed

a striking contrast of red nucleoli and centrosomes, with black osmophile granules.

One unfertilized oöcyte, first order, contained eleven nucleoli (?) distributed in and near the spindle and throughout the cytoplasm. The acid fuchsin was subsequently removed from these structures with 70% alcohol, and they could no longer be seen without the aid of sketches to indicate their position, while the black osmophile granules remained as sharply differentiated as before. In unstained preparations (such as described above) we have found these granules at all stages of the development of the egg, from the smallest oöcytes (or oögonia) to the segmenting ova, and in the former, one is occasionally found so exactly in the center of the yolk nucleus that in a stained preparation it would be unhesitatingly pronounced a centrosome. Tiny osmophile granules are often seen within the attraction spheres, spindle, and cones, though they are *far more* numerous throughout the rest of the cytoplasm. In some cases one, two, or more osmophile granules have been seen apparently in the exact center of a sphere (Text-fig. I). Throughout the rest of the cytoplasm, both their distribution and form vary greatly, even at exactly the same stage of the development of the egg. As to distribution, they are sometimes quite evenly distributed throughout the cytoplasm (Text-fig. I), and again large areas appear to be entirely free from them. As to size, they are sometimes tiny microsomes (Photo. 8 and Text-fig. I), and again many of them are as large and homogeneous as nucleoli (Photo. 12), while in many cases they appear as masses — aggregations of individual granules (Photo. 13). Whether any one of these conditions is distinctive of the normal egg we are unable to determine at present.

There are equally marked variations in their response to stains ; after a short immersion, iron haematoxylin removes the blackening caused by osmic fixatives — and, as a rule, it does not stain the granules. After prolonged immersion (three days) the osmophile granules show only a faint indication of the stain, and in these cases, when mounted in xylol balsam, they entirely dissolve out of the sections (*cf.* Photos. 13 and 14). In exceptional cases, however, they have formed an insoluble compound

with the stain and cannot be dissolved out. Photo. 9 is a section of an ovarian egg, in which these granules stained intensely with iron haematoxylin, all the sections in this slide giving the same reaction. The next slide of sections of the *same ovary* was treated similarly, and the osmophile granules did not stain.

In a few cases we have completed the entire process of killing, sectioning, staining, and mounting, within ten hours; and in these cases the granules have responded sharply to the stain, but we have not repeated this method often enough to test its value.

*Formation of Vesicles between First and Second Maturation Spindles.* — In earlier papers (4-6) one of us has stated that at the telophase of both the first and second maturation spindles, the chromosomes assume the form of small vesicles, corresponding in number to the number of the chromosomes.

Mead (8) has seen in *Chaetopterus* similar vesicles at the telophase of the second maturation spindle. He describes the formation of these as follows: "When the chromosomes have reached a position near the poles of the spindle, each of them swells up to form a vesicle, in which, at first, two distinct rows of granules may be seen. Later, each chromosome exactly resembles a miniature nucleus." Whether the chromosomes of the second maturation spindle of *Allolobophora foetida* form their vesicles in this way, we are unable to state, as we have not yet secured preparations of the second maturation spindle showing the metamorphosis of the chromosomes to vesicles. Of the first maturation spindle, however, we have preparations showing these transitional stages, and they suggest a method of formation differing from that of the second maturation spindle of *Chaetopterus*. Text-fig. II represents a number of forms

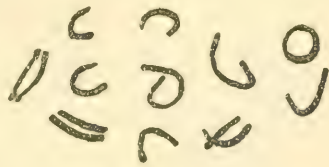


FIG. II. — Some forms shown by the chromosomes at the telophase of the first maturation spindle, showing the probable method of formation of the eleven vesicles, which are present a little later. Camera, Zeiss 2 mm. immer., oc. 22. Cf. Photo. 11.

assumed by the daughter-chromosomes of the tetrads of the first spindle. At the telophase of this spindle (Photo. 11) we find these forms both in the polar body and egg. They

suggest that the vesicles of this stage are formed by the two parts of each chromosome uniting to form a ring.

*Living Cytoplasm.* — The cytoplasm of the living egg of *Allolobophora foetida* presents a dissimilar structure at different stages of its development, and it has been our aim to demonstrate this difference and to determine, if possible, what structures in the sections can be identified with those seen in the living egg.

In an egg at the pronuclear and first cleavage stages we have a definite cytoplasmic feature, which is not so pronounced in the less mature egg. This feature is conspicuously shown in Photo. 1 in the form of globules of varying sizes,

which appear to be an approximately transparent non-miscible substance suggesting drops of sap or oil. We have designated them as sap globules rather than oil globules, as they do not blacken with osmic.

In the living oöcyte, first order, we have not been able to demonstrate this structure (Text-fig. III), but in oöcyte second order we find very tiny sap globules (Text-fig. IV) which gradually increase in size as the egg matures (Photos. 4-5, I); (the globules developing whether the egg is fertilized or not).



FIG. IV. — Peripheral sap globules after formation of 1st polar body. Traced from photographic negative of living egg.  $\times 500$ .

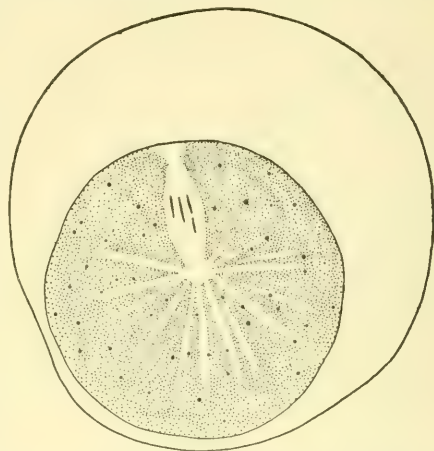


FIG. III. — Living unfertilized egg, from perfectly white cocoon. Only the larger osmophile granules represented. Chromosomes distinctly visible. Camera, 2 mm. immer., oc. 2.

In abnormal eggs the sap globules are relatively large — the early stages of a pathological condition being apparently expressed by a too rapid development of the cytoplasm. The normal enlargement of the globules, as expressed in later stages, cannot be due to individual growth, for the increase in the size of the egg is not at all commensurate with



the enlargement of the sap globules. It would seem, rather, that this sap, which in some form must also be present in oöcyte first order, is molded into the more definite shapes of the later stages by a rearrangement of the other constituents of the cytoplasm. If an egg is gently pressed until a tiny break is made in the outer membrane, the larger globules become somewhat constricted in form when flowing through this aperture as represented in Text-fig. V. After escaping from the pressure of the aperture, they regain their spherical shape.



FIG. V. — Sap globules pressed out of living egg. (Pronuclear stage.) Free-hand sketch. To the right a large globule has broken into several small ones. One of the large globules above is the result of the fusing of two smaller ones.

When an egg at the pronuclear stage has been kept in water too long, the globules fuse and swell, many of them increasing in size two or three times their diameter, giving the egg a vacuolated appearance.

This rapid and definite response to abnormal conditions suggested to us their value as a guide to determine the relatively harmful effect of killing fluids, for any fixative producing a marked disturbance of the sap globules or the surrounding substance would probably cause the globules to fuse or break up at once. Our method has been as follows (under a Zeiss 2 mm.): First, to focus on the periphery of an egg showing



FIG. VI.



FIG. VII.

FIG. VI. — *A.* Sap globules of living egg. *B.* The same globules after 15 minutes in 1 per cent. osmic. Zeiss 2 mm. immer., oc. 2 (camera).

FIG. VII. — *A.* Sap globules of living egg. *B.* The same area after 15 minutes in chromo-acetic. Zeiss 2 mm. immer., oc. 2 (camera).

pronounced sap globules, sketching about half a dozen of these with the aid of the camera (Text-fig. VI, *A*); second, one of us then applies the fixative, while the other closely watches the effect produced on the sap globules; third, after 15 to

30 minutes, the same globules are again sketched to illustrate the effect produced by the fixative (Text-fig. VI, *B*). A comparison of Text-figures VI and VII will show the relative injury to the form of the globules produced by 1% osmic acid and chromo-acetic. Photo. 3 further illustrates the effect of chromo-acetic on the sap globules and a comparison of this Photo. with Photos. 2 and 5 will show that osmic acid and corrosive sublimate are far less injurious. In Photo. 2 many of the sap globules in the center, and the line of globules on the right, were sketched from the living egg (camera lucida), and a comparison of the sketch with the photograph shows scarcely perceptible change in structure. Such changes as occur later in corrosive sublimate and osmic preparations are probably produced by the alcohols and imbedding. In order to test this we have fixed, stained, hardened, and cleared eggs under a Zeiss 2 mm. immer., oculars 2 and 4. We have repeated many times each step in the technique, selecting, as in the case when the fixative alone was tested, a definite number of sap globules upon which to center our attention. As, however, the egg becomes more opaque during the process of hardening, this method does not promise to be as satisfactory as a complete comparison of sections with freshly fixed material of the same stage. The above-mentioned method of applying the fixative while focusing on the periphery of the egg (under such gentle pressure that the egg continues to develop normally) has been supported by applying the fixative to a thinner layer of cytoplasm, obtained by gently pressing an egg until it is flattened to the outer membrane. The form of the sap globules remains unchanged under this pressure, and their reaction to the fixative appears to be the same as when the egg is not subjected to pressure. Whether any part of the sap globules becomes coagulated by the fixatives and takes part in forming the network seen in some sections we are unable to determine. If the globules are present in any form, they do not stain, for the vacuoles seen in the sections (Photos. 6, 16-18) undoubtedly answer to these structures. How far the breaking or fusing of the sap globules may be responsible for definite features of certain fixatives we are not prepared to answer until

we can support our conclusions with a larger number of photographs of sections.

In the living egg there appear to be at least four constituents of the cytoplasm.

1. The above-mentioned clear, approximately transparent sap globules of varying sizes (Photos. 1, 2, 4, 5).

2. Dense, opaque, deutoplasmic granules, varying in size from tiny points, scarcely visible under a magnification of one thousand diameters, to those plainly seen with the low powers. In form, size, and distribution they appear to answer to the above-mentioned osmophile granules (page 130) (Photos. 4, 5, 7-9, 12, 13, and Text-fig. I). These granules dance about with great activity in eggs that have been kept too long in artificial media — this abnormal activity being probably due to pathological disturbances in the rest of the cytoplasm.

3. Nucleolar-like bodies, strongly refractive in the living egg — that do not blacken with osmic. In the sections they react to the stains selected by the nucleoli of the pronuclei. The sperm-granules (4 and 6) react to the same stains.

4. Lighter areas which are relatively free from the sap globules and osmophile granules — these areas being represented by the polar rings, spindle, attraction sphere, and the interspaces of the sap globules. This substance does not blacken with osmic and appears distinctly granular in fixed eggs. It stains intensely, and in the sections appears more opaque than the rest of the cytoplasm — even in those cases where the osmophile granules are not dissolved or faded out. Thus the lighter areas of the living egg are the darker areas of the sections. (*Cf.* Text-fig. III and Photo. 17.) A study of the living egg suggests no fundamental difference between that part of those lighter areas which contributes to forming the polar rings, spindle, and sphere (archoplasm (5)), and the part occupying the interspaces of the globules. We have been able to demonstrate a difference by differential staining of the sections (5), thus far succeeding only with the double stains. We have, however, additional data on this point arguing strongly for the specific nature of archoplasm.

*Chromosomes in the Living Egg.* — The rarity of the cases in

which we have been able to see chromosomes within the spindle led us at first to think that the living eggs which showed this exceptional feature must be abnormal, for, as a rule, the chromosomes are not visible until the egg dies naturally, or is killed by a fixative. It was not until we were able to watch an egg develop normally after the chromosomes were seen, that we were convinced these exceptional cases were due to other causes. This does not appear to be wholly dependent upon the position of the spindle, for often in cases where the spindle is in the most favorable position, and clearly indicated, the chromosomes cannot be seen, even with the highest powers.

Text-fig. III represents a living oöcyte, first order, taken from a freshly deposited cocoon. The chromosomes at the metaphase were so distinct that two of them were readily traced with the camera. We watched this egg until it constricted off its first polar body, and then we killed it in chromo-acetic, stained and hardened it, and in every respect it appeared to be a normal oöcyte, second order. We would accentuate the fact that the chromosomes in the living egg showed exactly the same form as those seen in sections, as this possibly indicates that the chromosomes are less sensitive than the cytoplasm to the action of the fixatives. The fact that these centers of activity are more staple than the cytoplasm, one of us suggested in a former paper (7), where it was stated that the pronuclei continued to develop long after the cytoplasm was unquestionably abnormal.

The egg represented in Text-fig. III was below the average in size, thus transmitting relatively more light; this fact probably accounting, in part, for the relatively distinct outlines of the structures within the egg. The broad, clear rays, which could be traced from the attraction sphere almost to the periphery, do not appear to correspond to the rays so clearly outlined in chromo-acetic sections (Photo. 15), but rather to those of osmic acid sections (Photo. 17). This photograph is technically poor, owing to the fact that it is taken from a section  $10\mu$  thick. It is introduced only because it is the best example we have (in sections) of a structure that can be compared to the rays of an attraction sphere in the living egg. We are not yet pre-



pared to discuss the finer details of these structures, for we feel we must wait until we can control the shrinkage of the eggs killed in osmic acid, before placing much confidence in the morphological details seen in sections. This shrinkage occurs in the alcohols. When formalin is substituted as a hardener, the shrinkage is much reduced, but the use of formalin prohibits sharp staining. The spinning phenomena, which has been seen by Mrs. Andrews (1) during the formation of the polar bodies in other eggs, we have not yet been able to detect, but in view of the exceptional cases in which we have seen the chromosomes and other details in the living egg of *Allolobophora foetida*, we are not prepared to say that the above-mentioned spinning phenomenon does not occur.

*Shrinkage.*—A comparison of the size of sections of eggs at a given stage with the size of the average living egg at the same stage shows that, at some point or points in the technique, a large amount of shrinkage has occurred, in some cases amounting to one-half the diameter of the living eggs. With a view to determine when the shrinkage occurs, we have first measured the living egg and then each step in the subsequent technique. In this manner we have tested twenty-eight fixatives, the compound fixatives and their component parts, each in varying strengths and varying the time the egg was immersed in the fixative from five minutes to twenty-four hours. An attempt to formulate the data gathered from these experiments has shown that the action of a given fixative upon eggs, even at the same stage of development, is extremely inconstant. But as a general rule, subject to many exceptions, it may be said: First, certain fixatives shrink the living egg, and in these cases relatively little shrinkage is produced by the subsequent treatment with the alcohols, *e.g.*, strong chromic acid and, in most cases, corrosive acetic (strong). Second, certain fixatives do not shrink the living egg, and in these cases they shrink more or less during the subsequent treatment with alcohols, *e.g.*, weak osmic acid, .1% to 1%, and corrosive sublimate. Third, certain fixatives swell the living egg, the subsequent treatment with alcohols producing a slight shrinkage—the final result being a mounted egg with almost the same diameter as the

living, *e.g.*, chromo-acetic,<sup>1</sup> strong osmic acid, platinum chloride. Fourth, the amount of shrinkage caused by the fixative is dependent upon the stage of development reached by the egg, the unfertilized egg being much more sensitive to the fixative.

The hundreds of eggs that we have measured have served merely to impress us with the fact of the inconstant effect of the fixatives and subsequent technique—this inconstancy speaking for the individuality of each egg. As shrinkage must be an important factor in determining the final distribution of the cytoplasmic elements, we hope to be able to collect enough data on this point to be of service.

#### PHOTOMICROGRAPHY.

*Preface.*—In the autumn of 1893 and the winter of 1894, my friend Dr. Charles G. Fuller, of Chicago, successfully photographed a full series of my sections of the egg of *Allolobophora foetida*, illustrating successive steps in the maturation and fertilization of the egg.<sup>2</sup>

The work was done with the Zeiss horizontal photomicrographic camera, Zeiss microscope with apochromatic condenser, Zeiss projection oculars 2 and 4, and Zeiss apochromatic lenses 16–2 mm. immer., 140 aperture. Artificial light was used. I am glad of this opportunity to express my indebtedness to Dr. Fuller. The good quality of his work will speak for itself when the photographs are published.

These photographs were shown at Woods Holl in the summer and early autumn of 1894, and, as far as I am aware, they were the first photomicrographs of sections showing the processes of maturation and fertilization of the egg.—KATHARINE FOOT.

Our work has been done with a Bausch and Lomb vertical photomicrographic camera, Zeiss microscope, apochromatic

<sup>1</sup>In 1896 (5) I regarded chromo-acetic as the most reliable fixative, giving as one reason for this, that eggs measured before killing, and after mounting, gave almost the same diameter. At that time I had not measured the eggs at *each step* in the *technique*, and the measurements were not extended to sections. — K. FOOT.

<sup>2</sup>As these photographs have no especial bearing on the details discussed in this preliminary, I shall reserve their publication for a future paper.

lenses 16-2 mm. immer., 140 aperture, Zeiss compensating and projection oculars. We have not used a magnification beyond one thousand, finding this will reproduce details that can be clearly seen only with a 2 mm. immer. and ocular 8.

With a 2 mm. immer. projection ocular 4, diaphragm of ocular at 0, and the longest draw, the magnification attained is nearly one thousand [about 960]. When the diaphragm of projection ocular 4 is adjusted to 10, the magnification is much less; *e.g.*, a draw giving a magnification of 520, with the ocular adjusted at 10, will give a magnification of 670, with adjustment at 0. We tested our magnification by measuring the object with a Zeiss micrometer eye-piece, then taking the measure of the photograph in microns, and dividing the latter by the former. On account of the difference in magnification dependent upon the adjustment of the projection ocular, we found this the only accurate method. Light — clear daylight; sun shining, but not on mirror. Time — as near noon as convenient. Exposure — as a rule, fifteen to thirty seconds for sections.<sup>1</sup>

It gives us pleasure to express our indebtedness to Prof. Henry Crew, of Northwestern University, for recommending to us the following methods of developing and printing; and for instruction in their use. Plates — Seed 27. Developer — Metol. Printing paper — Kirkland's Lithium.

We wish also to express our obligation to Mr. J. G. Hubbard for our first lessons in developing and printing.

The experiments of a year with photomicrography have convinced us of its utility as a practical aid in cytological investigation, and we hope in this paper to argue for its more general adoption. The impossibility of photographing fine cytological details, which can be readily illustrated by a drawing, has been urged by Flemming (3) and others as the principal argument against the use of the camera in cytological work, Wilson's atlas (9) and Erlanger's photographs (2) serving to support these objections.

Those who have attempted to photograph cytological details

<sup>1</sup> For photography by daylight it is necessary to have a time shutter in the camera.



realize the following technical difficulties. At a magnification of one thousand, which is often necessary to bring out these details, not enough light can be transmitted through our thinnest sections to admit of focusing delicate structures on the ground glass of the camera; *e.g.*, even with the aid of the best focusing glass the small centrosome shown in Photo. 15 cannot possibly be seen on the ground glass. It is barely possible to see this detail through the microscope with a 2 mm. immer. and ocular 8, and we were astonished to find it so distinctly reproduced in the photograph. The ring chromosomes in Photo. 11 further illustrate this point.

It is impossible, however, to focus such details on the ground glass, and it has been our aim to devise some method of overcoming this difficulty by discarding the ground glass as a factor in focusing.

Selecting a structure that could be clearly focused on the ground glass at a magnification of one thousand (a sharply stained nucleolus, for example), we first focused through the microscope, making a note of the exact position of the pointer on the face of the micrometer screw. We then slipped the camera down, focusing the nucleolus on the ground glass. The position of the pointer on the micrometer screw then indicated exactly the difference between the two foci. In order to facilitate the accurate measurement of this variation in focus we marked off into twenty parts each of the twenty-five divisions that are designated on the face of the micrometer screw. The difference in focus proved to be about  $\frac{3}{20}$  of one of the twenty-five divisions; *e.g.*, with the pointer at the 5 mark for the focus through the microscope, to get the focus on the ground glass, turn the screw until the pointer indicates 4 and  $\frac{17}{20}$ .

We have tested the accuracy of this method by photographing at 960 diameters such a detail as the centrosome in Photo. 15. We took five photographs in as many minutes, keeping all the factors unchanged except the focus. One photograph was taken at what we calculated to be the correct focus; *i.e.*,  $\frac{3}{20}$  above the focus through the microscope. Two were taken above this point and two below. Trying this several



times, we found that the variation of  $\frac{3}{20}$  almost unfailingly caught the desired focus.

As two or three photographs can be taken in as many minutes, we generally take three of each preparation, one at the tested focus, one  $\frac{1}{20}$  above, and one  $\frac{1}{20}$  below this point, in case any difference in temperature, thickness of the cedar oil, or any other unforeseen factor should affect the focus. The few minutes required to develop these extra negatives is time well spent, for occasionally the focus above or below the tested one proves the best. This variation in focus can be just as readily settled for any magnification, and it does away entirely with the hopeless effort of attempting to focus fine details on the ground glass. We have tested the method with different magnifications and different lenses, and find it works admirably in all combinations, but it seems unnecessary to give figures for the different tests, as the variation is undoubtedly a point that must be settled for each microscope.

A method of work that can aid the biologist in seizing accurately and rapidly any points of interest his material offers, and enables him to retain them in a form convenient for comparative study, must certainly be of great value in the laboratory. Photomicrography appears to us to fill just such a need. A dozen photographs of a variety of features can be taken in the time required to reproduce any one of them by a careful drawing. The printed photographs can be kept in a form serviceable for frequent reference, and the impression first made by the preparation not allowed to fade. Possibly a photograph is less intelligible than a simplified sketch to any one unfamiliar with the preparation, but cannot this be said of the preparation itself? We have collected over two hundred sketches and as many photographs, illustrating features in our sections we wished to preserve for comparative study. Of the relative values of these two methods there can be no question, in every case the photographs proving to be the more valuable aid in recalling the preparations. We are not pleading to replace the sketch with the photograph, but we would argue for the use of both, letting the photograph speak for the preparation and the

sketch for the investigator's interpretation. One of the criticisms of Erlanger's photograph, most commonly heard, emphasizes the worthlessness of his preparations. Is not this the strongest possible argument in favor of photomicrography?

WOODS HOLL, October 10, 1898.

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## EXPLANATION OF PLATE A.

THE reproductions for the following plates were made by Edward Bierstadt of New York. His work was so admirably done that neither strength nor definition has been sacrificed by the process of reproduction.

In order to economize space, only a small portion of the negatives of Nos. 1-5, 10, 11, 13-15, has been reproduced. The eggs of Nos. 2-5, 10, were fixed under a Zeiss 2 mm. immer., one of us applying the fixative while the other watched its effects. All the photographs were taken with Zeiss 2 mm. immer. projection ocular 4.

PHOTO. 1. Living egg (stage, telophase of first cleavage spindle). Periphery of egg, showing part of a polar ring, surrounded by sap globules. Egg slightly colored with weak methyl green. The negative of this egg being a little sharper, it was chosen in place of one of an unstained egg of the same stage. In these cases the light was transmitted through a part of the egg fully 100  $\mu$  thick; thus a very sharp negative could scarcely be expected.  $\times 500$ . Medium, distilled water.

PHOTO. 2. Periphery of a segmenting egg, after 20 minutes in corrosive sublimate. Delafield haematoxylin. Before killing the egg, many of the sap globules were sketched with the camera lucida, including the line of five on the right. The fixative produced no perceptible change in their size or contour. (*Cf.* No. 5.)  $\times 500$ . Medium, distilled water.

PHOTO. 3. Periphery of oöcyte, second order, after chromo-acetic (15 mm.). Stained with alum cochineal, hardened in alcohol and cleared in xylol. The small sap globules have fused, forming irregular patches.  $\times 500$ . Medium, xylol.

PHOTO. 4. Periphery of egg just after formation of second polar body. Slightly flattened. Killed in .1 % osmic acid (15 mm.). Gentian violet.  $\times 500$ . Medium, distilled water. *Cf.* size of sap globules with those of egg of a little later stage (No. 5).

PHOTO. 5. Periphery of egg at pronuclear stage. Pronuclei one-half maximum growth. Egg pressed until the cytoplasm reached the outer membrane. This was done under a 2 mm. immer., and the sap globules appeared neither broken nor fused by the gentle pressure. A comparison of the photograph with a living egg at the same stage shows them to be the normal size. 1% osmic acid, 1 hour. Unstained.  $\times 500$ . Medium, distilled water. The sharp black specks are osmophile granules; those out of focus appear as faint rings.

PHOTO. 6. Section (4  $\mu$ ) through cytoplasm and one polar-ring of egg at telophase of first cleavage spindle. Fixative, chromo-acetic. Hardened in 40 % formaldehyde, 26 hours. Stain, iron hæmatoxylin.  $\times 340$ . Medium, xylol balsam.



PLATE A.







## EXPLANATION OF PLATE B.

PHOTO. 7. A small piece of the cytoplasm of an oöcyte, second order. Unstained. The egg was killed in 1% osmic, and after one hour crushed on the slide. This was to demonstrate the presence of the osmophile granules to compare with those of No. 9.  $\times 900$ . Medium, distilled water.

PHOTO. 8. Ditto. Changing focus in order to reproduce the three tiny granules, two on the left and one on the right of the preparation. In No. 7 the two on the left (out of focus) appear as tiny faint rings.

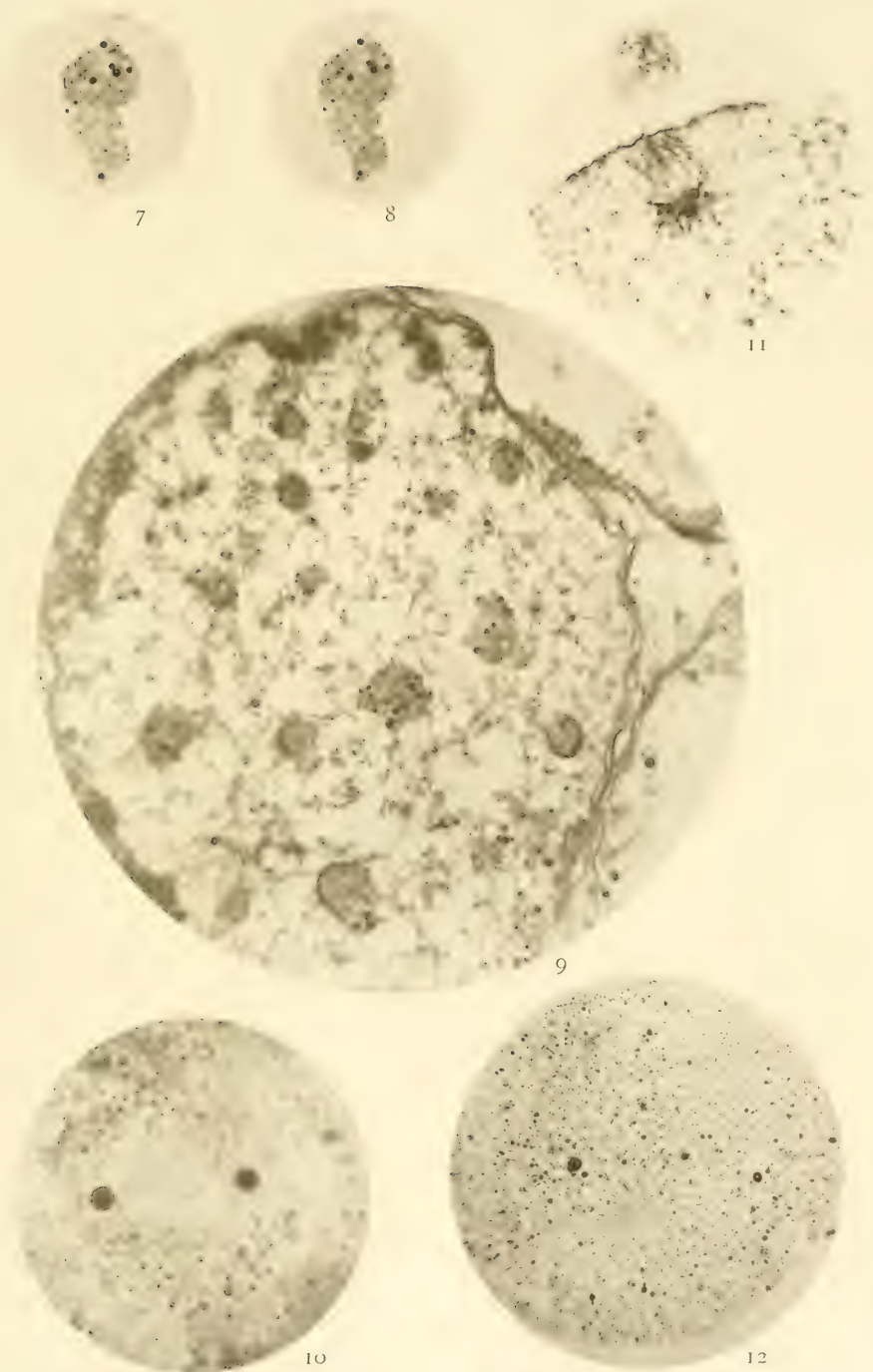
PHOTO. 9. Section ( $3\ \mu$ ) through the cytoplasm of an ovarian egg at free end of ovary. Granular aggregations of archoplasm and osmophile granules, such as are found in the oögonia or tiniest oöcytes, and in eggs of later stages, both in the ovary and cocoon. Cf. Nos. 4, 5, 7, 8, 10, 12, 13. Fixative, chromo-acetic followed by osmic. Hardened in alcohol, 24 hours. Iron haematoxylin.  $\times 860$ . Medium, xylol balsam.

PHOTO. 10. Nucleus in a macromere of a segmenting egg, showing two nucleoli and chromatic thread. Fixed under Zeiss 2 mm. immer., 1% osmic acid. Delafield haematoxylin. Exposure  $1\ \frac{1}{2}$  minutes, as the light was transmitted through the entire egg.  $\times 900$ . Medium, distilled water.

PHOTO. 11. Section ( $3\ \mu$ ) of telophase of first maturation spindle. Cf. Text-fig. II. Fixative, chromo-acetic. Hardened in 5% formaldehyde, 48 hours. Iron haematoxylin.  $\times 860$ . Medium, xylol balsam.

PHOTO. 12. Section ( $3\ \mu$ ) of oöcyte, second order. Killed in chromo-acetic, washed in water, followed by 1% osmic acid for 30 minutes, to differentiate the osmophile granules. Hardened in alcohol. Unstained.  $\times 500$ . Medium, glycerine. Cf. Text-fig. I. Attraction sphere and the refractive sperm indicated, although the egg is unstained.









## EXPLANATION OF PLATE C.

PHOTO. 13. Section ( $4\ \mu$ ) through cytoplasm of oöcyte, second order. About one-third of the negative reproduced. Fixative, Hermann. Hardened in 10% formaldehyde, 21 hours. Unstained.  $\times 870$ . Medium, glycerine. The photograph was taken to demonstrate the two aggregations of osmophile granules, and the smaller ones throughout the cytoplasm. Cf. No. 14, which is the same section, after staining in iron haematoxylin 24 hours, and dissolving out the osmophile granules with xylol and xylol balsam. A careful comparison of the two photographs will show that they are focused on the same plane, the stained preparation, however, showing no trace of the black granules demonstrated in the unstained section. No. 14 shows that the stain has differentiated certain granules that are not seen at all, or are very faintly indicated in the unstained preparation. The section was finally stained deeply with methyl green, with the view of determining whether any granules could be differentiated within the vacant places formerly occupied by the black osmophile granules. None could be seen.

PHOTO. 14. See No. 13.

PHOTO. 15. Section ( $4\ \mu$ ) through upper pole of first maturation spindle. A centrosome in the sphere, and equally sharply stained granules beyond the sphere. Fixative, chromo-acetic. Hardened in alcohol. Iron haematoxylin.  $\times 960$ . Medium, xylol balsam.

PHOTO. 16. Section ( $3\ \mu$ )<sup>1</sup> of egg at pronuclear stage, showing a part of one of the pronuclei which have attained about one-half their maximum growth. (After other fixatives, the pronuclei have a very different appearance.) Aggregations of archoplasm (polar-ring substance) at periphery; possibly some of the same substance around the pronucleus. Fixative, .2% osmic. Hardened in 5% formaldehyde, 22 hours. Iron haematoxylin, 28 hours.  $\times 540$ . Medium, xylol balsam.

PHOTO. 17. A very thick section ( $10\ \mu$ ) of an oöcyte, first order. Lower pole of first maturation spindle, and an indication of the chromosomes which are approaching the lower pole (spindle at anaphase). This section was photographed merely because it showed thick rays from the attraction sphere, which strongly suggest those seen in the living egg (represented in Text-fig. III, at a little earlier stage). The sap globules in this egg are larger than is the rule in normal eggs at this stage. No. 18 is the following section photographed to show the row of sap globules completely surrounding the attraction sphere, and to compare this attraction sphere with that of Photograph 15, in which case the egg was killed in chromo-acetic. Fixative, 1% osmic acid. Hardened in alcohol. Iron haematoxylin.  $\times 500$ . Medium, xylol balsam.

PHOTO. 18. See No. 17.

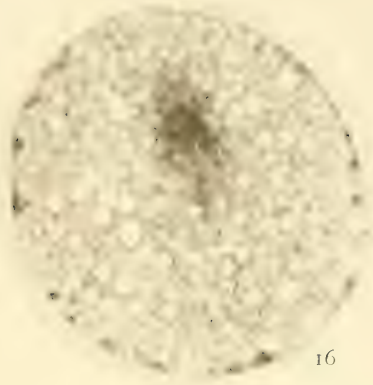
<sup>1</sup> We have tested the accuracy of our microtome by measuring the diameter of the eggs, both before and after sectioning, and counting the number of sections; e.g., this section is one of a series of thirty, and the largest of these measures  $94\ \mu$  in diameter.



PLATE C.



13



16



14



17



15



18



## ZOÖLOGICAL BULLETIN.

NOTES ON THE OCCIPITAL REGION OF THE  
TROUT, *TRUTTA FARIO*.

M. A. WILLCOX, Ph.D.

PROFESSOR OF ZOÖLOGY IN WELLESLEY COLLEGE.

ABOUT a year and a half ago I undertook an investigation for the purpose of determining the number of segments in the hinder part of the head in the Teleostei. Only when the work was nearly complete did it come to my attention that Harrison, in his paper entitled "Die Entwicklung der unpaaren und paari-gen Flossen der Teleostier," had covered much of my ground. Under these circumstances it seemed unwise to continue the investigation. But as my results embody a few new points, I give herewith a brief summary of them.

The material was obtained from the Zürich fish breeding station and consisted of eggs of the salmon, *Salmo salar*, and the trout, *Trutta fario*. When they came into my hands, the salmon eggs had already been developing twenty-nine days in water of 10° Centigrade, and required twenty-eight days in water of about 7°–8°<sup>1</sup> to hatch. The age of the trout eggs was unknown, but I estimated them to be about four days older; they required twenty-two days in water of about 7°–8° to hatch. The material was preserved in an aqueous solution of corrosive sublimate, to which was added 20% of glacial acetic acid; it was then imbedded in paraffin, sectioned, and stained with haemalum. The greater part of the work was done upon the trout, the salmon being used only for comparison.

<sup>1</sup>The temperature was not determined at the time, so that this is merely an approximate estimate based upon the observations of others.

I take as the basis of my description the youngest of the trout embryos. The following data will indicate their approximate age: The length was a little less than 1 cm.; the spinal ganglia were formed, but the anterior ones were still connected by a longitudinal commissure with the vagus; the operculum had covered the first branchial arch. The characteristic structures of a segment at this stage are: (*a*) a pair of myotomes; (*b*) a spinal nerve with a ventral root and a dorsal ganglion which is not as yet directly connected with the spinal cord by a dorsal root; (*c*) a portion of condensed mesoblast forming the anlage of the axial skeleton. These structures I will take up successively in order to compare the condition in the most anterior segments with that which obtains farther back.

The myotomes are well differentiated and in general similar; they extend forward to the foramen for the vagus, the first one lying close behind the condensed mesoderm which invests the ear. Striation of the fibers is already present but is not uniform, being generally more pronounced in the deeper parts. The time at which striation appears seems to be variable; in a second specimen nine days older than this it is barely indicated.

The anterior three myotomes lie laterad of the parachordals and accordingly represent post-otic cephalic segments; they resemble the posterior ones but lie more laterad, as if pushed out by the enlargement which forms the hind brain. In front of the lateral portion of the most anterior one on the right side is a small triangular mass of tissue in which a few unstriated longitudinally disposed muscular fibers are to be seen, and which undoubtedly represents another nearly atrophied myotome, *making the number of post-otic cephalic segments four*. I propose at the earliest opportunity to examine younger embryos in the hope of finding this first myotome better developed. In salmon embryos I have found no trace of it, though I have not made a search exhaustive enough to warrant me in asserting that it is absent. In trout embryos one day older than the one just described, it has disappeared; the succeeding (second) myotome pair also eventually atrophies, though I am unable to say just when. Seven days after hatching it shows no trace of degeneration; in trout of fourteen days it has entirely dis-



appeared. It undoubtedly corresponds to the temporary myotome pair found by Harrison in *Salmo*.

The anlage of the axial skeleton consists at this time of condensed mesoderm aggregated on either side of the chorda, especially along the dorso-lateral and ventro-lateral lines, extending up the neural canal nearly to the top of the spinal ganglia and broadening anteriorly into the parachordals. This anterior broadening begins opposite the fifth myotome. The mesoderm shows no trace of segmentation, except that it is marked at intervals by ridge-like vertical thickenings corresponding to the myosepta. Such ridges are present also on the parachordals opposite the myosepta between segments 2 and 3, 3 and 4, 4 and 5. Cartilage is present in an embryo nine days older; it has the form of paired rods (neural arches) flanking the spinal cord. Each rod lies with its ventral end in a myoseptum, but crosses the myotome obliquely, so that its dorsal end lies in or near the next anterior myoseptum. The foremost rods cross the fifth myotome pair; they are considerably smaller than the others, and are closely connected by condensed mesoderm with the parachordals. They are obviously the anlage of the neural arch (occipitalbogen), which in the Salmonidae fuses with the skull. In specimens of twenty-one days after hatching, no fusion has yet taken place. The parachordals in my youngest embryos are largely chondrified; the cartilage exists as a continuous mass which shows no suggestion of segmentation. According to Stöhr, that portion which lies behind the otic capsules ("hintere Parachordalplatten") chondrifies on either side from a single center.

We come now to the nerves. The two temporary segments are altogether without them, but the first permanent segment has a rudimentary one; the second permanent segment has a typical spinal nerve which differs in no respect from the succeeding ones, and in my oldest embryos (twenty-one days after hatching) shows no sign of degeneration. Harrison states that in salmon somewhat older the dorsal root is atrophied. The rudimentary nerve of the first permanent segment is present in my youngest embryos. It is better developed on the right side, and here has the typical structure of a spinal nerve, differing

from the succeeding ones only in being much smaller. On the left the ventral root is wanting. On each side the dorsal ganglion is connected by a longitudinal commissure anteriorly with the ganglion of the vagus, posteriorly with the spinal ganglion of the next nerve. This rudimentary nerve has disappeared entirely, or, at most, has left only a trace in embryos nine days older; in those which have been hatched fourteen days, the nerve of the second permanent segment innervates also the first segment. This nerve and the one belonging to the next succeeding segment leave the neural canal by the

same foramen, namely, the one between the first neural arch and the parachordal. They correspond with those considered by Harrison to be the hypoglossal and the first dorsal. I have not traced their distribution, and am therefore unable to express an opinion on this point.

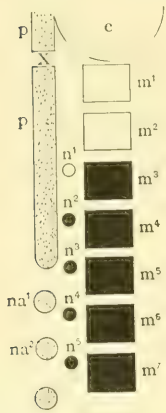


Diagram representing the changes which take place in the cephalic region of the trout between the fifth and tenth weeks of development. *e*, auditory organ; *m*<sup>1</sup>-*m*<sup>7</sup>, myotomes; *n*<sup>1</sup>-*n*<sup>5</sup>, spinal nerves; *na*<sup>1</sup>-*na*<sup>2</sup>, neural arches; *p*, parachordal; *X*, position of vagus. Shaded or dotted structures are permanent; those which are left light disappear in the course of development.

#### SUMMARY.

The cephalic region of the trout consists then of at least four segments. These are represented by more or less perfectly developed myotomes of which the first two pairs atrophy in the course of development. The skeletal anlage shows no trace of segmentation. The third segment has a rudimentary spinal nerve which early atrophies; the fourth has a typical one which three weeks after hatching shows no sign of degeneration. The condition cannot be better represented than by a diagram similar to that already employed by Sewertzoff.

This investigation was carried on in the laboratory of the University of Zürich, and I gladly take this opportunity of thanking Professor Lang for his kindly aid and interest, as well as for the generous way in which material was placed at my disposal.

## NOTES ON THE MUSHROOM BODIES OF THE INVERTEBRATES.

### A PRELIMINARY PAPER ON THE COMPARATIVE STUDY OF THE ARTHROPOD AND ANNELID BRAIN.

C. H. TURNER.

MUSHROOM bodies, fungiform bodies, pedunculated bodies, are synonyms that have been applied to certain peculiar structures found in the insect brain. These bodies were first discovered by Dujardin.<sup>1</sup> Although rediscovered by Leydig<sup>2</sup> and Rabl-Rueckhard,<sup>3</sup> yet aided by osmic acid, the microtome and staining fluids, Dietl<sup>4</sup> was the first to give a complete description of the whole organ. Thanks to the researches of more recent investigators, it is now well known that the mushroom bodies occur in all classes of insects, and that they reach their highest development in the *Hymenoptera*. Dietl,<sup>4</sup> Berger,<sup>5</sup> and Viallanes<sup>6</sup> have found in the *Decapod* brain structures which they consider homologues of the mushroom bodies of the *Hexapod* brain. Kenyon,<sup>7</sup> as the following quotation shows, thinks all of these men are mistaken. "Special swellings found on the brains of certain of the Crustacea have been compared to them (the mushroom bodies), but it is seriously doubted, I think, whether such swellings or cellular heaps are properly to

<sup>1</sup> Dujardin, "Mémoire sur le Systeme nerveux des Insects," *Ann. Sci. Nat.* Ser. 3, tome xiv, pp. 195 *et seq.*, Pl. IV. 1850.

<sup>2</sup> Leydig, *Vom Bau des thierischen Körpers.* pp. 232 *et seq.* 1864.

<sup>3</sup> Rabl-Rueckhard, "Studien über Insektengehirne," *Reichert und Du Bois-Raymond's Archiv. f. Anat.* pp. 488, 489. 1875.

<sup>4</sup> Dietl, "Die Organisation des Arthropodengehirns," *Zeit. f. wiss. Zool.* Bd. xxviii, pp. 488-517. 1876.

<sup>5</sup> Berger, "Untersuchungen über den Bau des Gehirns und der Retina der Arthropoden," *Arb. Zool. Inst. zu Wien.* Bd. i, Heft 2. 1878.

<sup>6</sup> Viallanes, H., "Étude Histologique et Organologique sur les Centres Nerveux et les Organs des Sens des Animaux Articulés," *Ann. Sci. Nat. Zool. et Pal.* Tome xiv, pp. 405-455, Pls. X, XI. 1893.

<sup>7</sup> Kenyon, F. C., "The Brain of the Bee," *Journ. of Comp. Neurology.* Vol. vi, pp. 133-210, Pls. XIV-XXII. 1896.

be homologized directly with them. In neither Retzius' figure of the brain of *Astacus fluviatilis*, nor in Bethe's figures of the brain of *Carcinus moenus*, can I find cells having the relations and the appearance of those I find in the bee. I have noticed

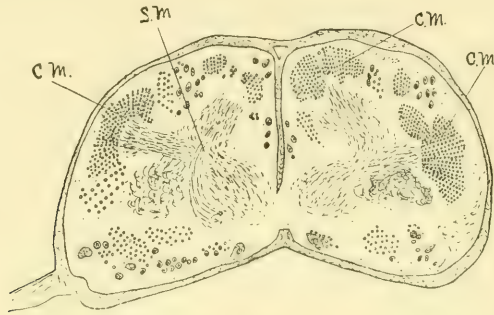


FIG. 1. — Section through the mushroom bodies of *Cecropia* larva.

nothing resembling the structures in Isopods or Amphipods, nor have I found indications of them in the brains of *Paupopus*, *Polyxenus*, *Scolopendrella*, *Lithobius*, nor even in several forms of *Thysanura* that I have examined. If cells homologous with those filling the cup-like calyx of the mushroom bodies of the bee are at all present in these forms, they are so undifferentiated as to be indistinguishable from the general mass of cells about them."

More recently Hamaker<sup>1</sup> has homologized certain groups of cells found in the brain of *Nereis* with the Hexapod mushroom



FIG. 2. — Section through the brain of *Cambarus*.

bodies. He bases this conclusion upon the following facts: (1) the cells of that type are confined to the brain; (2) they

<sup>1</sup> Hamaker, J. J., "The Nervous System of *Nereis virens* Sars," *Bull. Mus. of Comp. Zool. at Harvard College*. Vol. xxxii, No. 6. 1898.



are intimately connected with the neuropil; (3) they have small nuclei, and very little cytoplasm; (4) they are arranged in rows radiating from the neuropil.

While now at work upon a comparative study of the Arthropod and Annelid brain, several preparations have been examined which throw light upon the distribution of the mushroom bodies. Since it will be some time before these studies can be completed, certain discoveries bearing directly upon the distribution of the mushroom bodies are described in this preliminary paper.

The author does not consider this the place to record the bibliography, nor to discuss the technique, nor to acknowledge



FIG. 3. — Section through the brain of *Nereis*.

his indebtedness to those who have in any way aided him in these studies. All such information will be given in the final paper.

The mushroom bodies are composed of two factors, cells and fiber tracts. The cells are minute bodies having small nuclei and almost no cytoplasm. In this respect they resemble Deiter's corpuscles of the vertebrate brain. Compact masses of these cells crown each stalk. In these nidi the cells are arranged in rows which radiate from the top of each stalk. In each half of the brain the principal fibers of the mushroom bodies are collected in a stalk which lies, more or less erect, in a plane which cuts the longitudinal axis of the brain nearly at right angles. The top of each stalk may be either unbranched or bifurcated or ramosely branched. The lower portion of the stalk usually gives rise to two branches, one passing outwards (laterad) and the other inwards (mesad).

The preparations at my disposal make possible the demonstration of these bodies not only in the Hexapods (Fig. 1), but also in the Decapods (Fig. 2), and in the *Xiphosura*, and in cer-

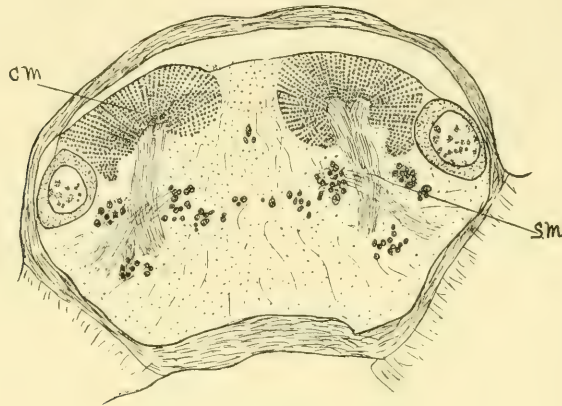


FIG. 4. — Section of *Polynoe*.

tain *Polychaeta* (Figs. 3-5), etc. In the *Polychaeta* the stalk seems to be unbranched (Fig. 5), although in *Nereis* (Fig. 3) and *Polynoe* (Fig. 4) there is a slight indication of a bifurcation; in the Hexapods (Fig. 1) and the Decapods (Fig. 2) it is bifur-

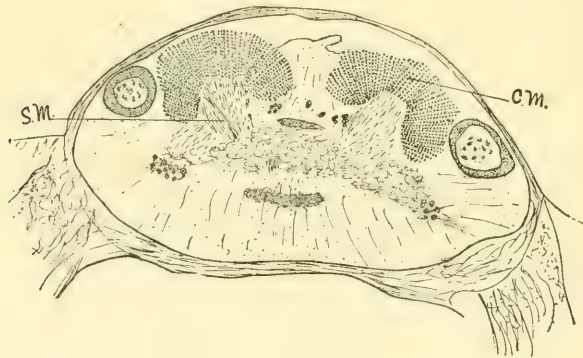


FIG. 5. — Section of *Lepidonotus*.

cated, while in *Limulus* (Fig. 6) it is ramose. Indeed, in *Limulus* it is so much branched that it simulates, in structure, the vertebrate cerebellum.

At present it is not possible to state whether these mush-

room bodies occur in all *Polychaeta* or not; but it is possible to assert that they exist in *Nereis*, *Lepidonotus*, and *Polynoe*. Nor is it possible to aver their existence in all Crustacea; but it is certain that they occur in *Cambarus* and *Limulus*. Both of these questions will be considered at length in the final paper to which is relegated a discussion of several fiber tracts connected with the mushroom bodies.

It is thought that sufficient facts and figures have been given to demonstrate that the mushroom bodies occur in the Hexapods, Decapods, *Xiphosura*, and certain *Polychaeta*. In each case these

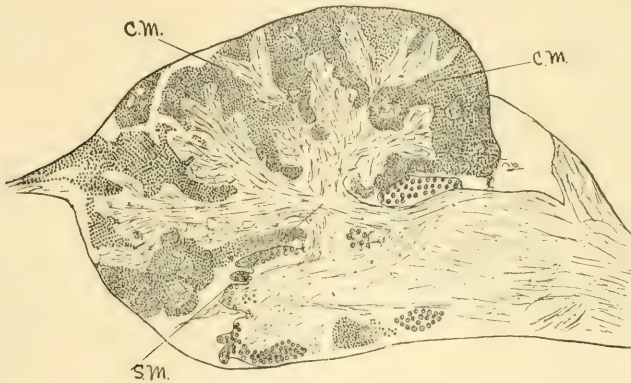


FIG. 6. — Sagittal section through the brain of *Limulus*.

bodies lie in the front portion of the supra-oesophageal ganglion. Is it not logical to conclude that the front portions of these brains are homologous? This statement runs counter to the generally accepted view. Goodrich,<sup>1</sup> who has recently investigated this question, does not think that the homologue of the Annelid prostomium, with its archicerebrum, occurs in either the insects or the Crustacea. But, since the mushroom bodies constitute the major portion of the protocerebrum of Hexapods and Decapods, and since the mushroom bodies occur also in the archicerebrum of certain *Polychaeta*, it follows that at least the major portion of the protocerebrum of the insects and the

<sup>1</sup> Goodrich, E. S., "On the Relation of the Arthropod Head to the Annelid Prostomium," *Quart. Journ. Micr. Sci.* Vol. xl, pt. ii, new series, pp. 247-268, 12 figs. 1897.

Crustacea is the homologue of the archicerebrum (supra-oesophageal ganglion) of the polychaete annelids.

CLARK UNIVERSITY, SOUTH ATLANTA, GA.

September 14, 1898.

#### REFERENCE LETTERS.

*C.M.*, cells of the mushroom bodies.

*S.M.*, stalk of the mushroom bodies.

All figures were drawn with a camera. Figures 2 and 6 are drawn to the same scale. Figures 3, 4, and 5 are drawn to the same scale, but are enlarged more than 2 and 6. Figure 1 is enlarged more than any of the others.



## NOTES ON NORTH-AMERICAN EARTHWORMS OF THE GENUS DIPLOCARDIA.

GUSTAV EISEN, PH.D.

WITH the discovery of a species of *Diplocardia* possessing the spermiducal pores in xx, it becomes advisable to include in this genus my genus, *Aleodrilus*. This genus was established some years ago for a species from Baja, California, *Aleodrilus Keyesi*, and based on the position of the spermiducal pores in xxi instead of in xix, as in *Diplocardia communis*, the only species known at that time. Later finds of new species of this genus show that *Diplocardia verrucosa* Ude stands intermediate between the two first-mentioned species, possessing the prostate pores in xx.

The location of the spermiducal pores in *Oligochaeta* is generally considered of generic importance, and it is very rare that we find variations in this respect in the same genus. But this character ought to be accompanied by others in order to serve as a genus characteristic, provided the distance between the respective somites is not very great. If we except the absence of penial setae in *Aleodrilus*, there are no other characters which would help to sustain the genus, since we have a complete series regarding the location of the male pores running through three successive somites. As few species of *Diplocardia* are known, and no confusion will ensue, a fusion of the two genera *Aleodrilus* and *Diplocardia* will help to simplify the already extensive nomenclature of the terrestrial *Oligochaeta*. Through the kindness of Prof. Frank Smith, I have had opportunity to examine all the various *Diplocardia* species at his disposal, and am able to add a few observations on minor points. I have also received several new species from North Carolina, which I describe here preliminarily, reserving a more detailed description for an illustrated paper now in press. As many more species of *Diplocardia* are likely to be found in the United States, a review of the species, so far known, is of

considerable interest, especially as the original descriptions are scattered, and not readily compared. I wish to call especial attention to the position of the spermathecal pores, which in some species are post-septal, in others pre-septal, while in at least one species some of the pores are pre-septal, while others are post-septal. The existence of sexual spermathecal setae is of the greatest interest. The sculptures of these setae vary in different species, and in a detailed description should be carefully noted.

Another interesting feature in the anatomy of at least one species, and probably in several, is the posterior "glandular crop" of the intestine, found in xiv and xv. It is of a totally different structure from the gizzard, and resembles greatly the glandular crop which I have once described in *Pontodrilus Michaelsoni*, and which in this species is also situated posteriorly.

With our extended knowledge of new species, it will be necessary to modify the definition of the genus as given by Ude, the last one to define the genus. Several of the characters considered by him generic are now seen to be only specific.

In the following I have endeavored to mark the thickening of some septa in a way that it could be readily recognized. The number of bars above the Roman numeral indicates the comparative thickness of the septa. Thus, one marked with three bars is about three times thicker than the one marked with one bar, etc.

#### DIPLOCARDIA GARMAN.

*Definition.* — *Setae*, eight, in four couples, lateral and ventral. *Penial setae*, present or absent. *Spermathecal setae*, present or absent. *Prostomium* divides somite i more or less. *Clitellum* saddle or ring like, generally xiii–xviii. *Oviducal pores* xiv. *Spermathecal pores*, two or three pairs, either post-septal or pre-septal. *Spermiducal pores* on xix, xx, or xxi, according to species. *Prostate pores* on somites next anterior and posterior to the spermiducal pores. The pores on each side connected by a groove. A *genital zone* generally present,

with or without papillae. *Intestine* with two gizzards, generally in v, vi. *Oesophagus* either with or without folds containing calcic concretions, but never with calciferous diverticula, as in *Benhamia*. Sometimes a glandular crop in xiv and xv. *Sperm sacs*, one pair pre-septal in ix, one pair post-septal in xii. Two pairs testes in x, xi. Two pairs sperm funnels in x, xi. *Prostates*, two pairs, opening anteriorly and posteriorly to the sperm ducts. *Spermathecae*, two or three pairs, each one with a diverticulum near the center. *Dorsal vessel*, double or single. *Nephridia*, meganephridia, generally without coelomic mantle. *Acanthodrilidae*. As far as known, confined to the United States and to northern Mexico.

The genus *Diplocardia* differs thus from *Acanthodrilus* in having two successive gizzards, *Acanthodrilus* having only one. From *Benhamia*, which genus possesses two successive gizzards, three pairs of calciferous diverticula, and numerous micro-nephridia, *Diplocardia* is distinguished by its meganephridia, of which there are two in each somite, and by the absence of calciferous diverticula of the tubular intestine. From both *Benhamia* and *Acanthodrilus*, as well as from all other genera of the family, *Diplocardia* is characterized by the position of its male or spermiducal pores.

*Key to Species of Diplocardia.*

- I. Spermiducal pores in somite xxi, no penial setae. (*Aleodrilus*.)  
*Sp.* 1. *D. Keyesi* (Eisen).
- II. Spermiducal pores in somite xx.  
*Sp.* 2. *D. verrucosa* Ude.
- III. Spermiducal pores in xix.  
*A.* Spermathecae, two pairs.  
*Sp.* 3. Both pairs of spermathecal pores pre-septal, or posterior to the setae; sexual spermathecal setae present in viii and ix.  
*D. Eiseni* (Michaelson).  
*Sp.* 4. The pair of spermathecal pores in viii are post-septal; the pair in ix are pre-septal. Sexual spermathecal setae in viii and ix.  
*D. Michaelsoni* n. sp.  
*Sp.* 5. Both pairs of spermathecal pores are post-septal, sexual spermathecal setae in viii-x.  
*D. Udei* n. sp.  
*Sp.* 6. Both pairs of spermathecal pores are post-septal, no sexual spermathecal setae.  
*D. riparia* Smith.

*B. Spermathecae, three pairs.**Sp. 7.* Penial setae straight, about one-half longer than ordinary setae.*D. communis* Garman.*Sp. 8.* Penial setae sigmoid, several times longer than ordinary setae.*a.* Penial setae not ornamented.*D. singularis* Ude.*β.* Penial setae ornamented. *D. singularis*, subsp. n. *caroliniana*.

## DIPLOCARDIA KEYESI (EISEN).

*Definition.* — *Color*, flesh, marbled violet, no pigment. *Size*, 70 mm. by 5 mm. *Somites*, 150. *Prostomium* divides somite i about one-half. *Dorsal pores*, the most anterior one in i viii/ix. *Spermiducal pores* in xxi. *Spermathecal pores*, two pairs, in viii and ix, in front of setae *ab*. *Prostate pores* in xx, xxii. *Oviducal pores* in front of setae *a*. *Setae* all ventral; *a-b* slightly larger than *c-d*; *a-a* larger than *b-c*. No sculpture. *Penial setae* none. *Spermathecal setae* not differentiated. *Clitellum* ring-like anteriorly, posteriorly saddle-shaped. *Genital zone* not distinct, two parallel grooves in  $\frac{1}{2}$  xx– $\frac{1}{2}$  xxii; groove almost straight, with a knob at each apex; concavity turned ventrally. *Septa*, thickened are :

$$\overline{\text{vi/vii}}, \overline{\text{vii/viii}}, \overline{\text{viii/ix}}, \overline{\text{ix/x}}, \overline{\text{x/xi}}.$$

*Oesophagus* without calcic concretions. *Gizzards* v, vi. *Sacculated intestine* xv. *Dorsal vessel* single, not covered with chloragogen cells. *Hearts* in x, xi, xii, with large pulsating divisions; no chloragogen cells. *Nephridia*, meganephridia, no coelomic mantle. *Testes* x, xi. *Sperm funnels* x, xi. *Sperm ducts*, which join at xii/xiii in a common muscular sheath; fuse in xx/xxi. *Sperm sacs*, one pair pre-septal in ix, one pair post-septal in xii. *Sperm masses* in x, xi. *Oviducts* in xiv. *Prostates* confined to one somite each, small, tubular, thicker at apex. *Spermathecae*, two pairs in viii, ix; distal end knob-like; the duct is very slender and long, with a very minute wart-like and ear-shaped diverticle, about the middle of the duct.

*Habitat.* — Ensenada de Todos Santos, Baja California, Mexico.

## DIPLOCARDIA VERRUCOSA UDE.

*Definition.* — *Color*, pink. *Size*, 65 to 75 mm. by  $2\frac{1}{2}$  to 3 mm. *Somites* 100 to 125, body round, of even thickness.



*Prostomium* divides somite i by one-half. *Dorsal pores*, most anterior one viii/ix (or x/xi). *Spermiducal pores* on xx. *Spermathecal pores* on anterior  $\frac{1}{3}$  of somites ix, x, somewhat dorsal to setae *d*. *Prostate pores* on xix, xxi. *Oviducal pores* interior to setae *a*, no glandular ridge. *Setae* sigmoid, very faintly ornamented. Distance *d-d* more than  $\frac{1}{2}$  the periphery; *c-d* somewhat larger than *a-b*; *a-a* three times, and *b-b* two and a half times larger than *a-b*, no setae *ab* in xx. *Penial setae* curved, not ornamented. *Spermathecal setae* not differentiated. *Clitellum* saddle-shaped, xiii–xviii. *Genital zone*, a rectangular field from posterior  $\frac{1}{3}$  xviii– $\frac{1}{2}$  xxii, extending laterally to center between *b-c*. Two deep grooves from  $\frac{1}{2}$  xix– $\frac{1}{2}$  xxi, the convexity of which is outwards, except in the center of xx, where it is turned towards median line; one median papilla on xxii; one pair papillae on xix in line with setae *b*; one pair papillae on xix and xxi, interior to grooves; one pair papillae exterior to grooves on each of xix, xxi, xxii (two pairs papillae on each of xix, xxi, and three papillae on xxii). *Septa*, thickened are:

$$\overline{\text{vi/vii}}, \overline{\text{vii/viii}}, \overline{\text{viii/ix}}, \overline{\text{ix/x}}, \overline{\text{x/xi}}, \overline{\text{xi/xii}}.$$

*Oesophagus*, no calciferous folds or thickenings. *Gizzards* in v, vi. *Sacculated intestine* commences in xvi. *Dorsal vessel* single. *Hearts*, three pairs in x, xi, xii. *Nephridia*, meganephridia, commence in ii, pores intersegmental in front of setae *d*. *Testes*, x, xi. *Sperm funnels*, x, xi. *Sperm ducts* open in central part of groove in xx. *Sperm sacs*, one pair pre-septal in ix, one pair post-septal in xii. *Oviducts* open in front of and interior to setae *a*. *Prostates* very thin, even, bent in four folds, confined to one somite each. *Spermathecae*, two pairs in viii, ix, retort-like, with a small, short-stalked, ear-like diverticulum below the center. No specialized spermathecal setae.

*Habitat*. — Omaha, Nebraska. (See note on page 172.)

#### DIPLOCARDIA EISENI (MICHAELSEN).

*Definition*. — *Color*, dorsally gray or pigmented, clitellum violet gray. *Size*, 150 mm. by 2 mm. *Somites*, 165; viii–xiii, smoother and wider than the others. *Prostomium* divides somite

i about one-half, with the lateral margins strongly converging. *Dorsal pores*, most anterior one on xi, first distinct one on xiii. *Spermiducal pores* on xix in line with setae *a*. *Spermathecal pores* viii, ix, posterior to setae *a*, in line with *ab*. *Prostate pores* xviii, xx, in line with setae *b*. *Oviducal pores* near median line, surrounded by a zone. *Setae*, sigmoid, with numerous fine bars; *a-a* about  $\frac{1}{12}$ , *d-d*,  $\frac{5}{9}$  the whole periphery; *b-c* is shorter than *a-a*; *a-b*, shorter than *c-d*; *a-b*,  $\frac{1}{2}$  as long as *b-c*; *a-b*, slightly shorter than *c-d*. Setae *b* in xix is present, *a* is absent or present. *Penial setae* rudimentary or very small, in the body wall of xviii and xx. *Spermathecal setae* differentiated and ornamented in viii and ix. *Clitellum* ring-shaped in xiii-xvii, saddle-shaped in xviii. *Genital zone*, a quadrangular glandular ventral zone in xviii-xx, in the corners of which lie the prostate pores. The two grooves are curved ventrally. No depressed area and no papillae. *Septa*, thickened are :

$\overline{\text{vi/vii}}, \overline{\text{vii/viii}}, \overline{\text{viii/ix}}, \overline{\text{ix/x}}, \overline{\text{x/xi}}, \overline{\text{xi/xii}}.$

*Gizzards* v, vi. *Sacculated intestine* commences in xviii, a dorsal typhlosole. *Dorsal vessel* alternately double and single in vi-xv. *Hearts*, four pairs in x-xiii. *Nephridia*, meganephridia, commence in iii. *Testes* in x, xi. *Sperm funnels* x, xi. *Sperm ducts* join, but do not fuse until at the male pore in xx. *Sperm sacs*, one pair pre-septal in ix, one pair post-septal in xii. *Oviducts* large. *Prostates*, two pairs in viii, ix. A large sac-like part and a thinner, irregularly bent, muscular duct; a small, stalk-like diverticle with a knob-like apex.

*Habitat*. — Florida.

#### DIPLOCARDIA RIPARIA SMITH.

*Definition*. — *Color*, brown anteriorly and dorsally, clitellum dull coppery colored. *Size*, 220-250 mm. *Somites*, 136-157. *Prostomium* divides somite i by one-half. *Dorsal pores*, most anterior one on anterior margin of xi, near x/xi. *Spermiducal pores*, xix. *Spermathecal pores*, two pairs in viii, ix, anterior to setae *ab*. *Prostate pores*, xviii, xx. *Oviducal pores*, xiv. *Setae* as in *D. communis*, no ventral setae *ab* in xix. Distance

$a-a = b-c$ ;  $a-b$  very little larger than  $c-d$ . *Penial setae*, xviii, xx. *Spermathecal setae* not differentiated (?). *Clitellum* saddle-shaped in xiii-xviii. *Genital zone*, no rectangular ventral zone; a ventral depression in xvii-xxi, deepest in xviii and xx. A pair of crescent-shaped grooves curved ventrally, from center of xviii-xx. Two papillae very close to median line, between xxi/xx. One median papilla xvi/xvii, one pair papillae xvii/xviii, one pair papillae xx/xxi, one pair papillae xvii/xviii. *Gizzards* v, vi. *Sacculated intestine* commences xviii. *Dorsal vessel* single. *Nephridia*, meganephridia, a small pair in ii. *Testes* in x, xi. *Sperm funnels* x, xi. *Sperm sacs*, one pair pre-septal in ix, one pair post-septal in xii. *Prostates* xviii, xx. *Spermathecae*, two pairs in viii, ix, with a large ear-like diverticulum, which is very prominent and exteriorily slightly racemose. Anterior and posterior spermathecae are of the same size.

*Habitat*. — Havana, banks of Illinois River, Illinois, U. S. A.

#### DIPLOCARDIA MICHAELSENI *n. sp.*

*Definition*. — *Color*, flesh. *Size*, 45 mm. by 2 mm., hardly tapering posteriorly. *Somites*, 63. *Prostomium* divides somite i completely. *Dorsal pores*, most anterior iv/v. *Spermiducal pores* xix. *Spermathecal pores*, one pair pre-septal in ix, one pair post-septal and almost central or median in viii. *Prostate pores* xviii, xx. *Oviducal pores* xiv, in front of and anterior to setae *a*, close together. *Setae* all ventral;  $a-a = 3 a-b$ ;  $a-a$  about one-third larger than  $b-c$ ;  $b-c =$  about  $2 a-b$ . *Penial setae* present at spermiducal pore. *Spermathecal setae* present in viii, ix; setae *a* and *b* being differentiated and sculptured. *Clitellum* ring-like, dorsally xiii- $\frac{1}{2}$  xviii; ventrally xiv-xvii. *Genital zone*, a deep central, oval pit in xviii-xx, surrounded by an elevated ridge. A pear-shaped ventral and median papilla in xxi and  $\frac{1}{2}$  xxii, and a similar papilla in  $\frac{1}{2}$  xxii and xxiii. Grooves between prostate pores are straight. A pair of deep, round pits in posterior part of xvii. No paired papillae. *Septa*, thickened are:

$$\overline{\text{vi/vii}}, \overline{\text{vii/viii}}, \overline{\text{viii/ix}}, \overline{\text{ix/x}}, \overline{\text{x/xi}}, \overline{\text{xi/xxii}}.$$

*Oesophagus* straight or bent, not widening in any somite. *Gizzards* vi, vii. A large, thick glandular *crop* in xiv, xv. *Sacculated intestine* commences in xviii. *Dorsal vessel* swollen in xvi, xvii. Single (?). *Hearts* x, xi. *Nephridia*, meganephridia. *Testes* very large in x, xi. *Ovaries* are digitate. *Sperm funnels* in x, xi. *Sperm sacs*, three pairs, in ix, x, xii. Those in ix are pre-septal, those in x and xii are post-septal, in xi only sperm masses. *Oviducts* in xiv. *Prostates* occupy somites xvii-xxi, glandular part contains only one layer of cells, muscular duct folded, glandular part thick. *Spermathecae*, duct muscular, long, folded, pouch large in two divisions; a large, oval, exterior diverticle, pointed forwards. The spermathecae in viii open anterior to setae, those in ix open posterior to setae.

In this species, as in *D. Udei*, there are bundles of glands opening jointly in a pair of circular orifices in viii and ix, between the sexual spermathecal setae. These glands are interposed between the layers of the body wall and the epithelial cells, and run parallel with the longitudinal axis of the body. Their structure is described more in detail in a memoir soon to be published by the California Academy of Science, San Francisco.

*Habitat.* — Raleigh, North Carolina, U. S. A.

#### DIPLOCARDIA UDEI *n. sp.*

*Definition.* — *Color*, flesh, without any pigment; an even tint all around the body. *Size*, 70-90 mm. by 2 mm. at the widest part. *Somites*, 200-220. *Prostomium* divides somite i about two-thirds. *Dorsal pores*, most anterior one on anterior part of xi. *Spermiducal pores* in xix. *Spermathecal pores*, two pairs, in front of setae *b* on anterior part of viii and ix. *Prostate pores* in xviii, xx. *Oviducal pore* xiv. *Setae*: *a-a* = 3 *a-b*; *a-a* slightly smaller than *b-c*; *b-c* = 4 *a-b* (about); *c-d* not quite twice as wide as *a-b*; *d-d* greater than half the periphery. In viii, ix, x, *a-a* =  $1\frac{1}{2}$  *a-b*. *Penial setae* present, ornamented. *Spermathecal setae* differentiated in viii-x, highly ornamented, accompanied by glands in the body wall. *Clitellum* dorsally



xiii- $\frac{1}{2}$  xviii, ventrally xiii- $\frac{1}{2}$  xxi. *Genital zone*, a narrow, deep, rectangular depression, deeper than in any of the other species, surrounded by a thick, elevated ridge. *Tubercula pubertatis* in xix-xxi, a pair of papillae in xviii. *Septa*, thickened are :

$\overline{\text{vi/vii}}$ ,  $\overline{\text{vii/viii}}$ ,  $\overline{\text{viii/ix}}$ ,  $\overline{\text{ix/x}}$ ,  $\overline{\text{x/xi}}$ ,  $\overline{\text{xi/xii}}$ .

Most anterior septum iii/iv. *Oesophagus*, no dilations containing calcic concretions. *Gizzard* v, vi. *Sacculated intestine* commences in xvii. *Dorsal vessel* single, thickly covered with chloragogen cells. *Hearts* x-xii, with chloragogen cells. *Nephridia*, meganephridia, no coelomic mantle. *Testes* x, xi. *Sperm funnels* x, xi. *Sperm sacs*, one pre-septal in ix, one post-septal in xii, both racemose. *Oviducts* small. *Prostates* very short and thick, occupying two somites each. *Spermathecae*, with a diverticulum hidden in the wall of the spermathecae, not perceptible except in sections. Anterior spermathecae largest.

*Habitat*. — Raleigh, North Carolina, U. S. A.

#### DIPLOCARDIA COMMUNIS GARMAN.

*Definition*. — *Color*, flesh; *clitellum* dull yellow or flesh. *Size*, 300 mm. *Somites*, 123-165. *Prostomium* divides i by one-half. *Dorsal pores*, most anterior one x/xi. *Spermiducal pores*, xix. *Spermathecal pores*, three pairs in vii-ix, in line with a-b. *Prostate pores* xviii, xx. *Oviducal pores* close together in front of and interior to setae a-b. *Setae*, ventral, a-a slightly larger than b-c, not ornamented; no setae a-b in xix. *Penial setae* in xviii, xx, only slightly curved, smooth, one-third longer than ordinary setae. *Spermathecal setae* not differentiated. *Clitellum* saddle-shaped, xiii-xviii. *Genital zone*, *copulatory papillae*: one pair on xvii, one pair xx. *Copulatory grooves* on xviii-xx, curved towards the ventral median line. With or without a depressed zone. *Septa*, thickened are :

$\overline{\text{vi/vii}}$ ,  $\overline{\text{vii/viii}}$ ,  $\overline{\text{viii/ix}}$ ,  $\overline{\text{ix/x}}$ ,  $\overline{\text{x/xi}}$ .

*Oesophagus*, no calciferous folds. *Gizzard* v, vi. *Sacculated intestine* commences in xvii, a low typhlosole from xxiii-xl.

*Dorsal vessel* alternately double and single from vii backwards. *Hearts* x-xii. *Nephridia*, meganephridia, most anterior one in iii. *Testes* x, xi. *Sperm funnels* x, xi. *Sperm ducts* join only at the pore. *Sperm sacs* in ix pre-septal, in xii post-septal. *Prostates* long, slender, tubular, abruptly bent at the pore, sometimes extending over more than one somite. *Spermathecae*, three pairs in vii-ix, club-like, with an ear-shaped diverticle below the center.

*Habitat.* — Illinois, in black prairie soil.

#### DIPLOCARDIA SINGULARIS UDE.

*Definition.* — *Color*, flesh. *Size*, 65 mm. by 3 mm. *Prostomium* divides somite i about one-half. *Dorsal pores*, most anterior one vii/viii. *Spermiducal pores* xix. *Spermathecal pores*, three pairs, vi/vii, vii/viii, viii/ix. *Prostate pores* xviii, xx. *Oviducal pore* xiv, interior to setae *a*, surrounded by a glandular ridge. *Setae*, ventral, lateral, *d-d* greater than half the periphery; *a-a* larger than *b-c*; *c-d* somewhat larger than *a-b*; *a-b* about one-half as large as *b-c*; *l.i.* shorter than *v.i.*; *a-b* twice shorter than *l.i.* and three times shorter than *v.i.*; faintly ornamented at apex. No setae *a-b* in xix. *Penial setae* three times longer than the ordinary setae, curved, not ornamented. *Spermathecal setae* not differentiated. *Clitellum*, ring-like xiii- $\frac{1}{2}$  xvii, saddle-shaped  $\frac{1}{2}$  xvii-xviii. *Genital zone*, no rectangular field, two lunate grooves on  $\frac{1}{2}$  xviii- $\frac{1}{2}$  xx, convexity towards ventral median line. One pair papillae in xvii. One pair in xx. Sometimes with a deep oval zone in xvii- $\frac{1}{2}$  xxi (Smith's specimens). *Oesophagus* strongly twisted, bead-like in x-xiii, narrower in xiv-xvi, no calciferous folds. *Gizzards* v, vi. *Sacculated intestine* commences in xvii. *Dorsal vessel* single. *Hearts*, three pairs in x-xii; in iv-ix narrow vessels. *Meganephridia*, pores ventral to setae *d*. *Testes* x, xi. *Sperm funnels* x, xi. *Sperm sacs*, one pair in ix pre-septal, one pair in xii post-septal. *Prostates* with many folds at right angles. *Spermathecae*, three pairs in vii-ix, sac-like, with gradually narrowing duct, with oblong diverticle.

*Habitat.* — Danville and Havana, Illinois.

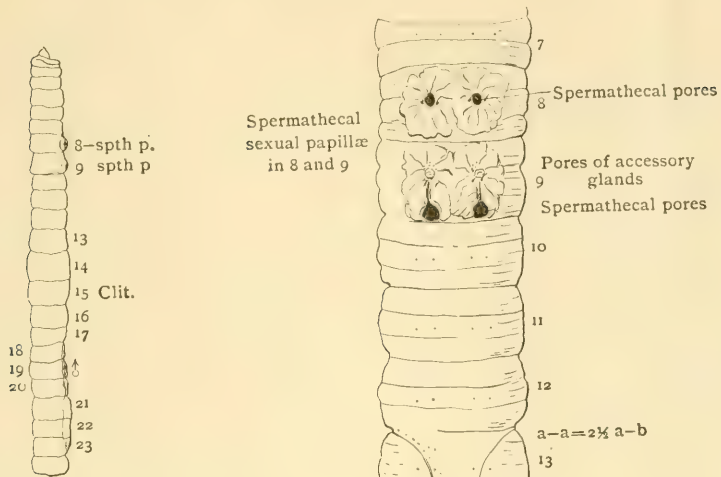


FIG. 1.



FIG. 2.

*Diplocardia Michaelsoni* n. sp.

FIG. 1.—Anterior part of worm seen from the side.

FIG. 2.—Ventral part of somites 7-24.

FIG. 3.—Tip of a spermathecal seta.

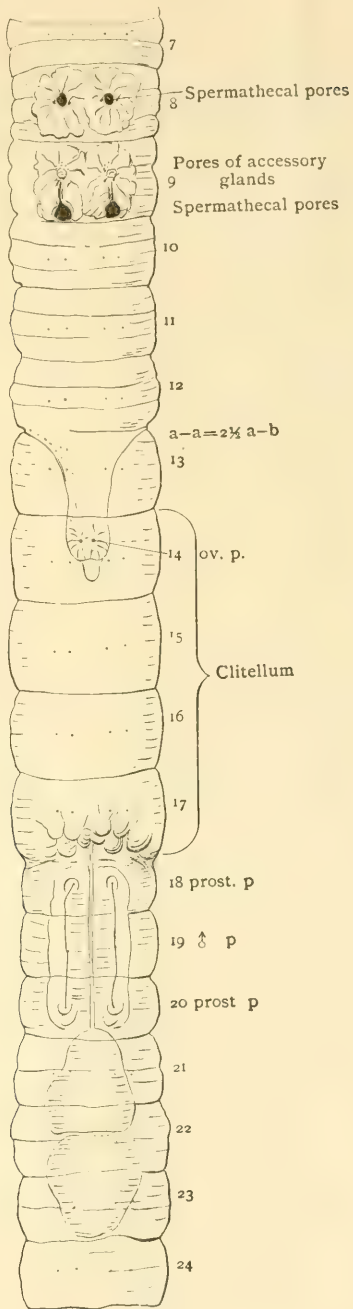


FIG. 3.

DIPLOCARDIA SINGULARIS (UDE), *subsp. n.* CAROLINIANA.

*Definition.*— *Color*, flesh, without pigmentation. *Size*, 40–50 mm. by  $1\frac{1}{2}$  mm. *Somites*, 64, 98–136. *Prostomium* divides i about one-half. *Dorsal pores*, most anterior on the front part of ix. *Spermiducal pores* xix. *Spermathecal* vii–ix. *Prostate pores* xviii, xx. *Oviducal pores* xiv, on a small glandular area. *Setae* as in the species, but *a–b* is about twice as long as *a–a*; *a–b* less than one-half as wide as *b–c*, all faintly sculptured. No setae *a–b* in xix. *Penial setae* curved, pointed, and ornamented. *Spermathecal setae* not differentiated. *Clitellum* ring-like, except in anterior part of xviii, where it is saddle-shaped, xiii– $\frac{1}{2}$  xviii. *Genital zone* not much differentiated. Two curved grooves, with the convexity turned to the ventral median line. In xvii two large circular areas, like depressed papillae. In xxi two similar areas. In xxii one median oblong area. *Septa*, thickened are:

$$\overline{\text{vii/viii}}, \overline{\text{viii/ix}}, \overline{\text{ix/x}}, \overline{\text{x/xi}}.$$

*Oesophagus* without calciferous folds. *Gizzards* v, vi. *Sacculated intestine* commences in xvii. *Dorsal vessel* single, with chloragogen cells. *Hearts*, muscular vessels in x–xii, with chloragogen cells. *Meganephridia*. *Testes* xxi. *Sperm funnels* x, xi, compact. *Sperm sacs*, one pair in ix pre-septal, one pair in xii post-septal. *Oviducts* with very large protruding funnels in xiii. *Prostates*, large, tubular, almost straight; one-third as wide as the body cavity. *Spermathecae*, three pairs in vii–ix. The anterior pair the smallest. The two posterior pairs the largest. Each of the latter extends through two somites backwards. The diverticulum is longitudinally oblong, with a distinct stalk or duct, and divided up in several chambers by trabecula.

*Habitat.*—Raleigh, North Carolina, U. S. A.

NOTE.—There is some little doubt about the opening of the spermathecae in *D. verrucosa*. Ude gives the pores as being slightly dorsal to setae *d*. Later, he says that the oviducal pores are also situated between setae *d*, while his Fig. 14 shows that they are situated between setae *a*. Of course it is possible that the misprint concerns only the reference to the oviducal pores. I have seen no specimens of this species. Those received from Prof. Frank Smith from Havana, Ill., and labeled "*D. verrucosa* Ude (?)" belong undoubtedly to a new, not yet described, species.



## NOTES ON THE FIRST CLEAVAGE OF LEPAS.

MAURICE A. BIGELOW.

ALL previous observers of the development of the Cirripede ova have agreed that the polar bodies are formed at the protoplasmic end of the ellipsoidal ovum. The first cleavage plane has usually been described as almost transverse to the long axis of the ovum. Ova in which the first cleavage plane was oblique and sometimes almost parallel to the long axis have been described as occasionally occurring. These have been regarded as variations from the normal cleavage. The conclusion has seemed unavoidable that the first cleavage plane is equatorial, and that it does not pass through the animal pole, as is the case in nearly all ova. Such are the conclusions of Groom ('94),<sup>1</sup> the latest investigator of the development of Cirripedia. The writer ('96)<sup>2</sup> found that in *Lepas fascicularis* the second polar body lies in the first cleavage furrow, the first one being outside the vitelline membrane. This position of the second polar body indicated that the first cleavage furrow passed through the animal pole of the ovum, but no observations were made which explained this position of the polar body apparently 90° removed from the point of its formation. Nussbaum ('87)<sup>3</sup> found similar relations existing in the ovum of *Pollicipes*, and assumed that the first cleavage furrow forms in the long axis of the ovum passing through the animal pole, and that it later rotates to the transverse position. The evidence which he offered in favor of his assumption was apparently shown to be incorrect by the subsequent observations of Groom.

In the course of comparative studies of the early develop-

<sup>1</sup> Groom, T. T. ('94), "Early Development of Cirripedia," *Phil. Trans.* Vol. clxxxv B, pp. 119-232.

<sup>2</sup> Bigelow, M. A. ('96), "Early Development of *Lepas fascicularis*," a preliminary note, *Anat. Anz.* Vol. xii, pp. 263-269.

<sup>3</sup> Nussbaum, M. ('87), "Vorläufiger Bericht," *Sitz. Berlin Akad.* 1887. pp. 1051-55. — ('90), "Anatomische Studien an Californischen Cirripeden." Bonn.

ment of several Cirripedia from the standpoint of cytogeny, the writer has recently been able to make observations on the living ova of *L. anatifera*, which explain the various conflicting observations and determine the relations of the first cleavage plane. Some mechanical effects have also been observed, which seem to contribute something of interest to the study of the mechanics of development. Some notes on the observations are given here; a detailed account with discussion is reserved for a future paper.

A brief description of the unsegmented ovum will serve as a basis for the discussion of the cleavage. The ovum of *L. ana-*

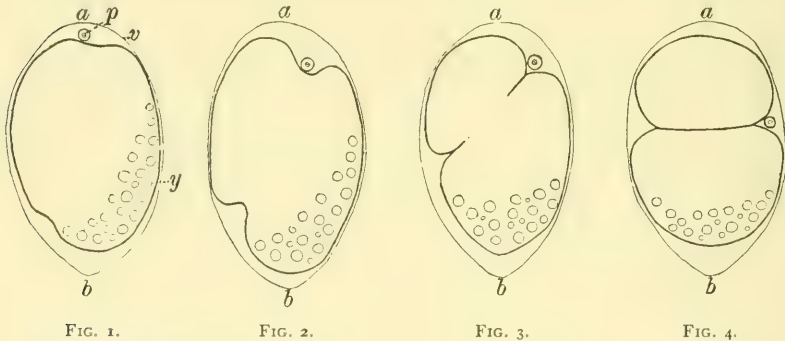


FIG. 1. FIG. 2. FIG. 3. FIG. 4.  
Camera drawings of the living ovum, showing the rotation of plane of cleavage. *a-b* marks the constant long axis of the vitelline membrane (*v.*), *p* indicates the second polar body, and *y* the yolk spherules.

*tifera* just before the beginning of cleavage is ellipsoidal in form. The yolk spherules at this time lie aggregated at one pole, which is known to be the ultimate posterior; but during the preparation for division the yolk shifts to one side of the polar area (Fig. 1). The vitelline membrane closely surrounding the ovum is rounded at the anterior and somewhat pointed at the posterior pole. It is apparently quite rigid and does not greatly alter in shape during the embryological development. The second polar body lies within the vitelline membrane at the anterior end of the ovum (Fig. 1).

Figs. 1-4 illustrate the changes in the external form of the ovum during the first cleavage. They are from camera lucida drawings of a living ovum, made at intervals of four minutes. They were selected from a series of fourteen drawings

made at intervals of one minute. The vitelline membrane occupied a fixed position with reference to lines on the slide and on the drawing board. The line *a-b* marks the long axis of the vitelline membrane, which before cleavage passed through the animal pole of the ovum. The cleavage furrow appeared in a plane passing through the animal pole and oblique to the long axis of the ovum (Fig. 1). As the cleavage furrow slowly deepened, the plane of cleavage rotated until, at the time of complete separation of the first two blastomeres, it was almost always transverse to the original long axis of the ovum; that is, it occupied a position at right angles to its first position, which was still clearly indicated by the unaltered form of the vitelline membrane (*a-b*, Fig. 4). In some ova observed the rotation was less, and at the close of the cleavage the plane of separation was oblique to the original long axis of the ovum. Such a condition would be well represented by Fig. 3, if the separation of the blastomeres were there shown as complete.

Along with this rotation of the cleavage plane there occurred a shifting of the position of the second polar body, which was in the cleavage furrow, and was followed to a position about  $90^\circ$  from the point of its formation (Figs. 1-4). Occasionally the polar body became detached from the ovum and failed to shift with the rotating furrow. This seems to explain the few cases observed by Groom, upon which he based his view that the first cleavage is usually formed transversely to the long axis of the ovum, and does not pass through the animal pole. Studies of the preserved material of several other species and genera lead me to believe that such a rotation takes place also in them. The polar bodies are formed in a position about  $90^\circ$  from that finally occupied by the first cleavage plane. There is reason for believing that this plane passes through the animal pole, for the second polar body is found in the cleavage furrow. The relations to the vitelline membrane are as in *L. anatifera*. These considerations make it very probable that in the case of all *Lepadidae* and *Balanidae*, whose development has been heretofore described, a rotation of the cleavage plane will be found to account for the apparently equatorial position of the first plane of cleavage.

A study of sections of the ova at various stages in the first cleavage shows that the mitotic spindle is at first oblique to the long axis of the ovum and nearly perpendicular to the plane in which the furrow first appears (Fig. 5). As cleavage progresses, the spindle turns with the plane of cleavage and at last comes to lie in the long axis of the partially divided ovum (Figs. 6 and 7). The amount of its rotation is approximately



FIG. 5.



FIG. 6.



FIG. 7.

Drawings of sections of ova in stages of cleavage corresponding approximately with those shown in Figs. 1, 2, and 4, respectively.

equal to that of the cleavage plane. From what follows it will appear that the rotation of the spindle is produced by the movement of the dividing cell-body.

The rotation of the first cleavage plane appears to be secondary to the cleavage processes and capable of an explanation along mechanical lines. The cleavage furrow appears in an almost longitudinal position, passing through the animal pole. As the furrow deepens, the forming cells tend to become spherical and hence lengthen the axis of the ovum perpendicular to the plane of cleavage. If no firm envelope confined the ovum and interfered with change in its form, the long axis of the two-cell stage would lie perpendicular to the plane in which cleavage begins; but the vitelline membrane evidently interferes with extension in this direction. As the cleavage progresses, therefore, and the resulting cells become more and more spherical (Figs. 2-3), a rotation of the ovum becomes necessary, for evidently the long axis of the two-cell stage must approximately coincide with that axis of the vitelline membrane. An examination of the figures makes it appear that, as the forming blastomeres become more spherical and consequently lengthen the



axis of the ovum perpendicular to the plane of cleavage, pressure is obliquely applied to the vitelline membrane with the result that the ovum as a whole rotates, and gradually the dividing ovum adjusts itself to the form of the vitelline membrane. The cleavage plane becomes transverse or oblique, depending upon the amount of rotation necessary to meet adjustment. With a relatively wide vitelline membrane the rotation is less than  $90^{\circ}$ , for the divided ovum can then become adjusted to an oblique axis of the membrane, and the cleavage plane consequently remains oblique.

The observations recorded above have been repeated on many ova from different individuals, so there can be no doubt that a normal condition is described.

MARINE BIOLOGICAL LABORATORY,  
WOODS HOLL, MASS.,  
August 30, 1898.



ON THE SPECIFIC IDENTITY OF COTYLASPIIS  
INSIGNIS LEIDY AND PLATYASPIIS  
ANODONTAE OSBORN.

CHARLES A. KOFOID.

Two species of trematodes belonging to the suborder *Aspidocotylea* and the family *Aspidobothridae* occur in this country as parasites of fresh-water clams. The first of these is the not uncommon *Aspidogaster conchicola*, described by von Baer ('27). This is an internal parasite infesting the pericardium, the liver, and the renal organ of many *Unionidae* of Europe and America. Its occurrence in this country was first reported by Leidy ('51, '57, and '58) in *Unionidae* from Pennsylvania. It has also been found in great abundance in various species of *Unio* and *Anodonta* from the Illinois River, examined at the Illinois Biological Station at Havana, during the last five years. On grounds which will be discussed later, Monticelli ('90) has raised the question as to the specific identity of the form reported by Leidy and the *Aspidogaster conchicola* of Europe. It seems probable, however, that Leidy had a form agreeing, in so far as he described it, with the European species as then known. My examination of the specimens from the Illinois River leaves no doubt in my mind that *Aspidogaster conchicola*, as further described by Voeltzkow and Stafford, occurs abundantly in that locality, and thus far no other species of this genus has been observed there, although over one thousand clams have been examined by Prof. H. M. Kelly and myself for these parasites. Under these circumstances the inference seems to be warranted that von Baer's *Aspidogaster conchicola* occurs in this country also, and is the common species, and the only one of the genus as yet found here.

The other trematode of this family which is a parasite of the *Unionidae*, is *Cotylaspis insignis* Leidy, and up to the present time it has been reported only from the *Unionidae* of the United

States, having been found by Leidy ('57 and '58) on *Anodonta fluviatilis* and *lacustris*, and by the writer, at the Illinois Biological Station, on *Unio alatus*, *anodontoides*, *confragosus*, *edentulus*, *elegans*, *gracilis*, *katharinae*, *ligamentinus*, *rectus*, *tuberculatus*, and on *Anodonta corpulenta*. Unlike *Aspidogaster*, it is an ectoparasite, being harbored in the mucus upon the surface of the host, upon the foot, the gills, and especially in the region of the axil and along the line of attachment of the inner gill to the body.

Ever since the publication of the original description of *Cotylaspis* there has been some question as to the standing of the genus founded to receive this one species; and, indeed, the validity of the species itself has been questioned at times. European helminthologists have assigned it various positions in the system, and have even reduced it to a synonym of *Aspidogaster conchicola*. This uncertainty and the resulting confusion in synonymy seem not to be due to the lack of illustrations and to the nature of the original description, for this, though brief, was concise, and accurate as far as it went, quite as full, indeed, as many specific descriptions by helminthologists of both continents at that day. It was rather the result of an opinion hazarded by Leidy ('58) that *Aspidogaster* and *Cotylaspis* might possibly represent "two different stages of existence of the same animal."

During the last four years the writer has had in course of preparation a paper on the structure of this interesting trematode. (See Forbes, '96.) It is the purpose of the present note merely to set forth the grounds on which Leidy's original description of the species is entitled to recognition and to discuss the synonymy briefly.

The first reference to this unique little trematode is in a brief note by Professor Leidy ('57) in the report of the proceedings of the Academy of Natural Sciences of Philadelphia for the meeting held Feb. 17, 1857. In the report of that meeting the recorder states that "Dr. Leidy made the following observations on *entozoa* found in the *Naiades*." (The italics are mine.) Strictly speaking, however, *Cotylaspis insignis* is an ectoparasite, as above stated, being found, as the note proceeds



to tell, "within the cleft of the upper branchial cavity, adhering to the outer surface of the renal organ and the continuous margin of the foot." The next year Dr. Leidy ('58) published the following more extended diagnosis of this new genus and species, allied to *Aspidogaster*:

*Cotylaspis* Leidy. — Body curved infundibuliform, anteriorly cylindro-conical, posteriorly expanding into a subcircular or oval ventral disc with numerous acetabula arranged in a triple series. Mouth infero-terminal, with a prominent upper lip, and protractile into a cup- or disc-like acetabulum. Intestinal apparatus as in *Aspidogaster*. Eyes two, distinct, black, situated on each side of the head. Generative apertures inferior, between the head and ventral disc.

*Cotylaspis insignis* Leidy, *Proc. Nat. Sci.*, 1857, 18. — Translucent white or pink white. Upper lip snout-like, conical. Ventral disc crenate at the margin; acetabula 29, oblong quadrate, the outer rows continuous in front and behind so as to form a circle. Length from  $\frac{1}{2}$  to 1 line; ventral disc from  $\frac{1}{4}$  to  $\frac{1}{2}$  a line in diameter.

*Habitation*. — Found adhering to the outer surface of the renal organ, and the upper margin of the foot, within the cleft of the upper branchial cavity of *Anodonta fluviatilis* and *A. lacustris*.

*Remarks*. — This curious parasite, though allied to *Aspidogaster conchicola*, is certainly distinct; and it never occupies the locality of the latter, which also is found in the pericardium of *Anodonta fluviatilis* and *A. lacustris*. It is an interesting fact that in accordance with its exterior position *Cotylaspis* possesses well-developed eyes, while the imprisoned *Aspidogaster* is blind. It has occurred to me that perhaps these two genera may represent two different stages of existence of the same animal.

Diesing ('59), in his *Revision*, recognized Leidy's genus *Cotylaspis*, associating it with *Aspidogaster*; Taschenberg ('79) recognized the genus, according it a position in the system between *Aspidogaster* and *Aspidocotyle*; and Hoyle ('88) also accepted the genus, associating it, as Taschenberg did, with the above-named genera. In 1885 Poirer described *Aspidogaster lenoiri* from the intestine of *Tetrathyra vaillantii*, a turtle from Senegal, but did not mention its striking similarity to *Cotylaspis insignis* in the general form, structure of the ventral sucker, and the gross anatomy which he briefly describes. Monticelli ('92) established a new genus, *Platyaspis*, for this peculiar species, but, with an interrogation point, made the closely related *Cotylaspis* a synonym of *Aspidogaster conchicola*, justifying this

disposition of the species by the doubt expressed by Leidy, and expanding the original describer's suggestion into a statement that *Cotylaspis insignis* may be the young of *Aspidogaster*. Inasmuch, however, as the species described by Leidy had eyes, and the young of *A. conchicola*, as described by Aubert ('55) and by Voeltzkow ('88), are not provided with these organs, Monticelli further suggests that the form found by Leidy in the pericardium of clams upon which *Cotylaspis insignis* was parasitic, and reported by him ('57, '58) as *Aspidogaster conchicola*, may not have been that species but another — by inference undescribed — American species of *Aspidogaster*. Braun ('89-'93) follows Monticelli ('92) in assigning Poirer's species *lenoiri* to the genus *Platyaspis*, though in the explanation of Figs. 1 and 2, Taf. xx, he refers to the species as *Aspidogaster lenoiri*. Because of this double designation Prof. H. L. Osborn's ('98) statement that "Braun ('92) in Bronn's *Klassen und Ordnungen* followed his [Poirer's] assignment of the animal to that genus" (*Aspidogaster*) is correct only for the plate designation) Braun also follows Monticelli in assigning *Cotylaspis insignis* to the genus *Aspidogaster*, but admits it to the list of valid species. He also cites Leidy's paper of 1857, but quotes (p. 896) his description of 1858.

Professor Osborn ('98) has recently described as *Platyaspis anodontae* a trematode which he has found on *Anodonta* (species not given) and *Unio luteolus* from Lake Chautauqua. This is, I believe, unquestionably Leidy's *Cotylaspis insignis*. Unfortunately, Professor Osborn does not discuss the relationship of the form which he has described as new, to the species found by Leidy, and does not even mention the genus *Cotylaspis* except when, by a curious *lapsus pennae*, he substitutes *Cotylaspis* for *Cotylogaster* in his reference (p. 56) to Monticelli's "paper on *Cotylaspis* in Leuckart's *Festschrift*." I fail to see in Professor Osborn's more extended account any disagreement with Leidy's original description, and a comparison of specimens shows that he is dealing with the same form that occurs at Havana, which I have referred to Leidy's *Cotylaspis*. From Professor Osborn's account of the animal and my own observations it follows that *Cotylaspis insignis* is a sexually mature animal

and not a larval stage of *Aspidogaster conchicola*, with which, as Leidy ('57, '58) reported, it is associated. I have found the eggs, the young in various stages, and the adults of *Cotylaspis*, but no trace of any evidence to support the conjectures of Leidy ('58) and Monticelli ('92) that *Cotylaspis* is one stage in the life cycle of *Aspidogaster*. The doubt raised by Leidy ('58) and amplified by Monticelli ('92) is thus removed, and the species as originally described by Leidy ('57) should be recognized. Furthermore, the ectoparasitic habit, the presence of eyes, and the presence, on the adult, of a ventral sucker containing a definite number of alveoli necessitate, to my mind, the rehabilitation of the genus *Cotylaspis* to receive this species. As Stafford ('96) has shown, a variable number of alveoli may be present in the ventral sucker of *Aspidogaster* when sexually mature.

The eyes of *Cotylaspis insignis* are very prominent in the adult, and their nervous connection with the cerebral mass can readily be demonstrated with methylen blue. Osborn's statement that in trematodes eyes "are not hitherto recorded of adults" is not strictly correct, since Braun, for example ('89-'93, pp. 464, 465, and 693), cites no less than fourteen different genera of the *Monogenea*, and one of the *Digena*, in which species occur whose adults have well-defined eyes.

*Cotylaspis insignis* is also peculiar in possessing, as does *Aspidogaster*, a series of so-called marginal sense organs, placed in the angles of the crenulate margin of the ventral sucker at the points where the partitions between the alveoli of the outer circle meet the outer wall. There are thus twenty of these peculiar organs in *Cotylaspis insignis*. Neither Leidy ('57, '58) nor Osborn ('98) mention these organs; they are, however, present in a specimen kindly loaned to me by the latter for comparison. The genus *Platyaspis*, as defined by Monticelli ('92) for the reception of Poirer's African species, has for one of its diagnostic characters the absence of these marginal sense organs. Poirer, however, in his original description makes no statement as to the presence or absence of these organs, and Monticelli ('92) and Braun ('89, '93) have taken this negative evidence as a warrant for their statement that the organs in question are absent. The points of contrast between the two

genera, as described, are the presence or absence of eyes, the number of alveoli in the ventral sucker (29 in *Cotylaspis* and 25 in *Platyaspis*), and the ectoparasitic habit of the one and the endoparasitic habit of the other. Here, again, the absence of eyes in *Platyaspis* is inferred from Poirer's silence upon the subject. The endoparasitic habit of *Platyaspis* may also be questioned, for turtles are wont to feed upon molluscs, and molluscan parasites have been found in the intestines of mollusc-eating vertebrates. For example, Stafford ('96) suggests on the basis of the variation in form observed by him in *Aspidogaster conchicola* that *A. limacoides* Diesing, from the intestines of European fishes, is only an *A. conchicola* which had been taken into the digestive tract of the fish with its food. Similarly I have myself found in the intestine of *Cyprinus carpio* and *Moxostoma macrolepidotum* specimens of *Aspidogaster* which externally do not differ from *A. conchicola*. Furthermore, in one instance they were found with a mass of the glochidia of *Anodonta* — a coincidence which suggests their source. However, the data at hand do not justify, to my mind, the reduction of *Platyaspis* to a synonym of *Cotylaspis*. Monticelli's genus should, for the present at least, be retained for the reception of Poirer's species. Should future investigation reduce the now considerable differences which separate the two forms, and render advisable the assignment of the two species, *C. insignis* and *B. lenoiri*, to the same genus, then Leidy's *Cotylaspis* will take precedence of Monticelli's *Platyaspis*.

I give below the synonymy of *Cotylaspis insignis*.

***Cotylaspis insignis* Leidy (1857).**

*Cotylaspis insignis* Leidy ('57).

*Cotylaspis insignis* Leidy ('58).

*Cotylaspis insignis* Diesing ('59).

*Cotylaspis insignis* Taschenberg ('79).

*Cotylaspis insignis* Hoyle ('88).

*Aspidogaster conchicola* (in part) Monticelli ('92).

*Aspidogaster insignis* Braun ('89-'93).

*Platyaspis anodontae* Osborn ('98).

In this note the aim has been to show that *Aspidogaster conchicola* occurs in this country; that *Cotylaspis insignis* Leidy



is a sexually mature form and not a stage in the life cycle of *A. conchicola* or of any other species; that on these grounds Leidy's designation is entitled to recognition; that *Platyaspis anodontae* Osborn is a synonym of *Cotylaspis insignis*; and that Monticelli's genus *Platyaspis* should not be reduced to a synonym of *Cotylaspis* from data at present available.

ILLINOIS STATE LABORATORY OF NATURAL HISTORY,  
UNIVERSITY OF ILLINOIS, URBANA, ILLINOIS.  
November 10, 1898.

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## A PECULIAR NUCLEAR ELEMENT IN THE MALE REPRODUCTIVE CELLS OF INSECTS.

C. E. McCLUNG.

IN working out the spermatogenesis of one of the Locustidae, *Xiphidium fasciatum*, a nuclear element not heretofore described arrested the attention of the writer, and will here be given preliminary notice in order that other investigators in the same line of work may be induced to look for it in their preparations. For the sake of convenience this structure will be called, provisionally, an accessory chromosome.

While but the one species has been studied and the appearance of the new element noted, a study of figures representing insect spermatogenesis indicates that it is not merely a specific character. Such an inspection of the figures given by different writers shows clearly that the body under discussion has been observed, but that its true character has not been recognized. The reason for this may be apparent later, when the changes it undergoes have been described. The truly remarkable and striking nature of the element and its obvious importance in the formation of the spermatozoön render a more thorough knowledge of it highly desirable.

In order to make clear the true character of the body, an account of its behavior in different stages of the maturation of the spermatozoön will be given, and then attention will be called to the most striking features distinguishing it.

As it first appears in the spermatogonia of *Xiphidium fasciatum*, there would be no hesitation in calling it a nucleolus except for its unusual situation on the surface of the nuclear vesicle. It is a small, irregularly rounded body, and lies immediately under the nuclear membrane (Fig. 1). Before the division figure is established, however, it takes on the form of a thread which becomes "U"-shaped (Fig. 2). Still further contraction ensues, and by the time of the metaphase the

thread has become very short and thick and is bent in the middle with an obtuse angle so as to resemble a boomerang. At this time, it may be observed lying at one side of the circle of chromosomes arranged in the equatorial plate, and plainly

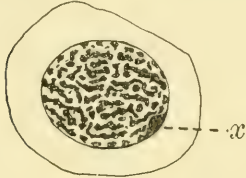


FIG. 1.— Prophase of spermatogonia showing the accessory chromosome, marked "x," applied to the surface of the nuclear vesicle.



FIG. 2.— Later prophase of the spermatogonial stage in which the accessory chromosome has become "U" shaped.

distinguishable from them by reason of its greater length (Fig. 3). From the pole the chromatin appears as a broad, fenestrated plate, and the accessory chromosome is indistinguishable from the ordinary ones (Fig. 4).<sup>1</sup> Because of the rapidity of the division none of the anaphases are to be seen, but in the telophases the ordinary chromosomes of the cell may be seen

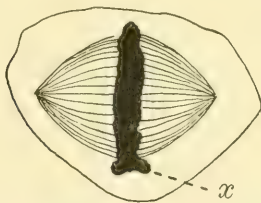


FIG. 3.— Metaphase of the spermatogonia showing the accessory chromosome applied to the periphery of the circle of chromosomes.



FIG. 4.— The same stage as represented in Fig. 3, but viewed from the pole.

grouped in the typical manner at the two ends of the spindle, while extending down towards the equatorial plate from each

<sup>1</sup> This peculiar arrangement of the chromatic mass is very striking, and is clearly due to a strong concentration of the nuclear elements. When the broad plate is cut squarely across, near one surface, the ends of the chromosomes may be observed as isolated bodies, but near the center of the group they lose their individuality in the mass. It is possible that the effect is due to improper fixation, but since all the cells around the follicle containing the spermatogonia, and even the cytoplasm of the spermatogonia themselves, is excellently preserved, this seems hardly probable.

mass is a half of the boomerang-shaped body which has been divided longitudinally in the same manner as the ordinary chromosomes. When this is observed projecting down from the middle of the group of chromosomes, thus presenting its broadest surface, it exhibits the form of an attenuated "U," the curved end of which is in contact with that of its fellow on the

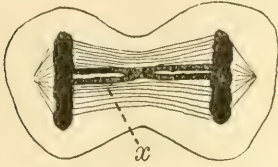


FIG. 5. — Late anaphase of the spermatogonia exhibiting the accessory chromosomes divided and still attached at their ends in the equatorial plate.

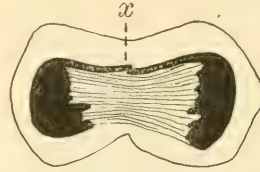


FIG. 6. — The same viewed from the side.

other side (Fig. 5). In cases where the section is cut so that the thread depends from the side of the group, the two chromatic masses present, roughly, the appearance of two hands with the index fingers pointing toward each other (Fig. 6).

In the resting stage of the spermatocyte that succeeds the appearance just described, the accessory chromosome again appears as it did in the resting stage of the spermatogonia, and

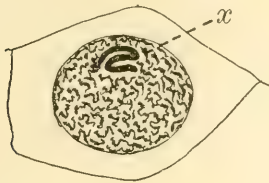


FIG. 7. — Early prophase of the spermatocyte. The accessory chromosome in the form of a coiled thread.

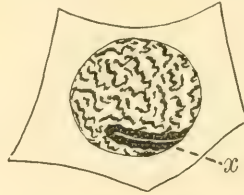


FIG. 8. — Later prophase of the spermatocyte. The accessory chromosome "U"-shaped.

would easily be taken for an ordinary nucleolus. Soon, however, it commences to assume a threadlike form which finally results in the production of a long "U"-shaped body, a form that is retained during the greater part of the spireme stage (Figs. 7-9). In this condition, it lies at the surface of the vesicle and stains in its usual intense manner. Concurrently with the formation of the "rings" from the spireme thread, it



commences to shorten and grows into the form of a horseshoe, and is finally to be distinguished from the chromatic rings only by its deeper staining quality and by the smoothness of its outline (Fig. 10). In the formation of the mitotic figure of the first spermatocyte division, it assumes its position on the outside of the group of chromosomes as it did in the spermatogonial division, and again has the boomerang shape that marked its appearance in the early figures (Fig. 11). When the chromatin

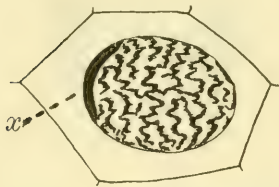


FIG. 9. — A somewhat later spermatocyte prophase. The accessory chromosome viewed from the side.

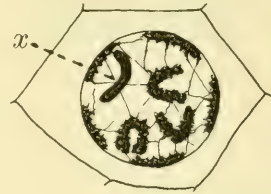


FIG. 10. — "Ring" stage of the spermatocyte. The accessory chromosome distinguishable from the remaining nuclear elements by reason of its greater density and smoother outline.

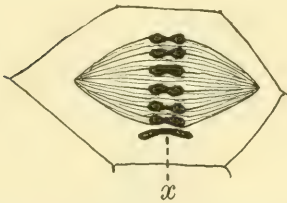


FIG. 11. — Metaphase of the spermatocyte. The accessory chromosome in the shape of a boomerang at one side of the group of chromosomes.

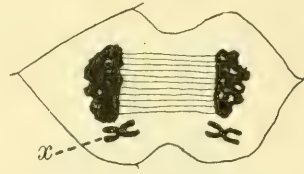


FIG. 12. — Late anaphase of the spermatocyte. The accessory chromosomes in the form of double horseshoes in the two daughter-cells.

separates and moves to the two poles, the accessory chromosome divides longitudinally and presents the appearance of two horseshoes with their rounded ends in contact (Fig. 12). In the second spermatocyte division, apparently the same process is followed.

The recently formed spermatids possess a nucleus in which the ordinary chromatin is extremely scant (Fig. 13) and very weak in staining power, while the accessory chromosome shows as prominently as ever and stains in the same uniform manner. It is not easy to trace out the part that the different elements

of the nucleus take in the formation of the spermatozoön, but in the light of present knowledge it appears as if the accessory chromosome was prominently concerned in the formation of the head. The nucleolus-like body that results from the last spermatocyte division, which has again taken up its position on the surface of the nucleus, becomes vacuolated and forms a covering for the nuclear vesicle. Gradually this collects at the end of the pear-shaped vesicle, and by the usual process of condensation and arrangement of the chromatic and achromatic parts of the cell the spermatozoön is formed.



FIG. 13. — Spermatid showing the strongly staining accessory chromosome and the weakly staining chromatin.

It being the purpose of the present article merely to call attention to the changes taking place in the accessory chromosome, no attention will be paid to the part played by the other cell structures, except as they have some bearing upon the behavior of this body.

In seeking to point out the features that characterize this peculiar nuclear element, perhaps the most striking thing to be noticed is the almost uniform staining power exhibited. While the ordinary chromatin gradually and progressively weakens in staining ability, the accessory chromosome retains its original affinity for the haematoxylin and basic anilines undiminished. As a consequence of this, in all the cells of the testes, the

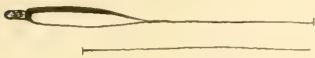


FIG. 14. — Almost mature spermatozoön.

accessory chromosome is at once distinguishable. Only in the early spermatogonia, when the chromatin stains most strongly, is there

any difficulty in observing this peculiar element. As the cells progress toward the formation of the spermatozoön, a greater and greater difference arises between the chromatin and its companion element, until in the spermatid so preponderant has become the volume of the accessory chromosome that one is almost irresistibly driven to the conclusion that it is chief in importance.

This variation in staining capacity of the chromatin and nucleolus (?) has not escaped the observation of other investigators. In describing the staining reaction of the different

elements of the testicular cells of *Caloptenus femur rubrum*, Wilcox<sup>1</sup> notes that, while ordinarily the chromatin and the nucleolus stain red and the cytoplasm green, by double staining in safranin and victoria green, yet "in *some*<sup>2</sup> stages the chromosomes were stained green, indicating that a chemical change takes place in the chromatic substance. But even in such cases the nucleolus was bright red."

Again, he states that "by this method (Henneguy's) the chromosomes and nucleoli are stained bright red." With reference to the changes occurring in *Cicada*, this alternation of staining power is noted particularly in the following language: "By the safranin and victoria green method the chromosomes stain red, though not so deeply as the nucleoli. At later stages the chromosomes assume a green color while the nucleoli continue to stain red. In still later stages the chromosomes again take the red."

All these color reactions ascribed to the nucleolus by Wilcox are strictly parallel to those exhibited by the accessory chromosome in *Xiphidium* preparations, and there can be little doubt that the two elements are identical. Added force is lent to this view by the appearance of the cells shown in Fig. 108 by Wilcox, in which the nucleolus is represented just as the accessory chromosome appears in the sperm-forming cells of *Xiphidium*. Moreover, with regard to the spermatogonial divisions, he says: "In most cases a nucleolus is to be seen during the prophases. In Fig. 106 there is in the nucleus a body (nucleolus (?)) which seems to have recently divided."

Later Wilcox refers to this same body, apparently, as a centrosome which becomes included in the nuclear membrane and goes to form the "neck" of the spermatozoön. He says:

"Some of the spermatids stained by Henneguy's method, and nearly all of those stained by Heidenhain's method, show a spherical body near the chromatic mass (Pl. V, Figs. 232-235), and this body becomes included in the nuclear vesicle when a membrane is formed (Pl. IV, Figs. 148 and 149; Pl. V, Figs.

<sup>1</sup> Wilcox ('95), "Spermatogenesis of *Caloptenus femur rubrum* and *Cicada tibicen*," *Contributions from the Zoöl. Lab. of the Mus. of Comp. Zoöl. at Harvard College*, vol. xxvii, No. 1.

<sup>2</sup> Italics in the original.

232 and 236). I regard this body as the centrosome which is left in each spermatid after the last spermatocyte division, and I also believe it to be identical with the very conspicuous body which forms the neck of the spermatozoön (Pl. V, Figs. 196–200). The chromatic substance fuses into a smoothly contoured mass, which soon assumes a crescent shape so common in insect spermatogenesis. The neck-body lies within the nuclear membrane opposite the concavity of the chromatic crescent (Figs. 198–200). The chromatin undergoes chemical and physical changes during the metamorphosis of the spermatid, but the neck-body remains practically the same in size, and does not alter its affinity for stains. It becomes the neck of the spermatozoön (Pl. IV, Figs. 139–158; Pl. V, Figs. 196–200). The chromatic crescent is at first less dense and stains less deeply; then it becomes concentrated, and stains nearly black by Heidenhain's method. These changes in density are not well shown in the figures. At the same time it becomes elongated, one end applying itself to the neck-body, the other becoming the tip of the spermatozoön head."

Although the writer has not yet had the opportunity to examine the cells of *Caloptenus*, he cannot but regard the views of Wilcox as erroneous. The close correspondence between the body which Wilcox designates, doubtfully, a nucleolus in one place and a centrosome in another, and the structure which has, in *Xiphidium*, been traced through the various developmental stages of the spermatozoön as an accessory chromosome, indicates that the phenomena of development are quite similar in the two cases. The centrosomes in *Xiphidium*, so far as observed, are quite small, and could in no case be mistaken for such objects as Wilcox represents in the cells of *Caloptenus*.

The absence of literature has prevented any further comparative study of the subject, unfortunately, but reference must be made to the figures of Henking<sup>1</sup> upon the spermatogenesis of *Pyrrochoris*, in which there seems to be something similar to the appearances found in *Xiphidium*. Figs. 16 and 17 show a body marked "n" that, so far as represented, might correspond to

<sup>1</sup> Henking ('91), "Erste Entwicklungsvorgänge in den Eiern der Insecten," *Zeit. f. wiss. Zool.*, Bd. li, p. 685.



the accessory chromosome of *Xiphidium* in the earlier stages of its formation. Again, in Figs. 40a, 40b, 41a, and 41b appears a nuclear element, marked "x," that is clearly to be distinguished from the other chromatic structures. The same element is traced through later stages, but its ultimate fate is not indicated.

Resembling the retarded separation of the accessory chromosome in the cells of *Xiphidium*, shown in Figs. 5 and 6, is that of a pair of chromosomes shown by Henking in his Figs. 55-58. These appearances certainly indicate a resemblance between insect seminal cells that is worthy of attention.

The figures accompanying this paper are diagrammatic, and are intended merely to show the one nuclear element in the various stages of its transformations. More detailed drawings will accompany a subsequent paper, in which will be recorded a general history of the male reproductive cells of *Xiphidium*.

#### TECHNICAL DETAILS.

The material employed in the investigation was collected in Chicago during the months of July and August. Nymphs having the wings but scarcely developed exhibited the most complete series of reproductive cells. To fix the tissues, Flemming's fluid, Hermann's fluid, corrosive-acetic mixture, platinic chloride solution, and chromic acid combined with formalin were employed. Osmic acid mixtures gave the best results, and were finally used to the exclusion of all other fixing agents.

Sections cut  $2\frac{1}{2}\mu$  and  $5\mu$  thick were fastened to the slide by the water method and stained in various combinations of colors. The most satisfactory preparations resulted from double staining by means of the iron-haematoxylin method of Heidenhain, followed by eosin for a plasmatic stain. Gentian violet and eosin also produced satisfactory images. Crushed, cover glass preparations, stained like the sections, proved valuable in the determination of details where the sections were not satisfactory.

Grateful acknowledgment is hereby made to Prof. W. M. Wheeler for suggesting the line of investigation and for valuable assistance rendered in the prosecution of the same. The



work was carried on in the Hull Zoölogical Laboratory of the University of Chicago during the summer of 1898.

THE UNIVERSITY OF KANSAS,  
LAWRENCE, KAN., December 1, 1898.

After the preceding had gone to press, a copy of Montgomery's paper<sup>1</sup> upon the spermatogenesis of *Pentatoma* was, by the kindness of Dr. Wheeler, placed at the disposal of the writer. In it is found a strong support of the views expressed in this paper upon the general character of the accessory chromosome—a support which strongly confirms the belief that this structure will be found very widely distributed, at least among the insects. Without doubt, however, specific variations of some magnitude will be found; the observations on *Pentatoma* and *Xiphidium* indicates this clearly. Much is therefore to be learned by a comparative study of different forms, and in this, objects such as *Xiphidium*, in which the element occurs with much prominence, will prove most valuable.

The results attained by Montgomery, however, are much in advance of any others up to the present time, and agree, in the main, with the appearances noted by the writer in the cells of *Xiphidium*. These are (1) the resemblance to a nucleolus in the resting stage, and (2) the similarity to a chromosome during the period of division. Montgomery expresses this briefly in the following language: "This peculiar structure acted like a nucleolus in the rest stage, but in the monaster is destined to lie in the equator among the chromosomes, where it also becomes divided in metakinesis, and so terminates by acting like a chromosome, as at the commencement it had been formed from one."

There can be no reasonable doubt of the accuracy of these observations when two investigators, working entirely independently of each other on different objects, reach the same conclusions.

<sup>1</sup> Montgomery ('98), The Spermatogenesis in *Pentatoma* up to the Formation of the Spermatid, *Zoologische Jahrbücher*, Abtheil. f. Anat. u. Ontog. der Thiere, Bd. xii.

While there exist these main points of agreement between the observations on *Pentatoma* and *Xiphidium*, minor differences may be noted. Thus there seems to be no reason to suppose that the accessory chromosome of *Xiphidium* arises by the direct transformation of one of the ordinary ones, although such a change may be possible. This does not argue against the chromatic origin of the body, however, for it is almost certainly modified chromatin, but in *Xiphidium* it arises during the resting stage and may represent derivative substance from one or all the chromosomes.

Again, its relative importance is much greater and its behavior more marked in *Xiphidium* than in *Pentatoma*. The constancy of form and structure appears to be less pronounced in Montgomery's object. As far as can be told, the staining reaction is essentially the same in both objects, and shows the same constancy that Wilcox noted for his "nucleolus." The final disposition of the body is a question that has not been decided in any case, and is one of great importance. It will, perhaps, require a knowledge of the steps in fertilization to decide positively the true character of the accessory chromosome.

Regarding the name to be applied to this structure, it would seem much more reasonable to class it with the chromosomes than with the nucleoli. The indefinite character of the latter group of bodies makes it desirable to avoid confusing the nomenclature by the addition of any more varieties to those already existing. But more important than this is the fact that during the time that chromosomes exist as such in the cell, the accessory chromosome is practically indistinguishable from the others in its behavior. It is a unit, a chromatic unit, constant in character and nearly typical in origin, transformation, and final disposition, as is believed, and corresponds well to the definition of a chromosome given by Montgomery, *i.e.*: "A chromosome is each separate chromatin element (chromatin microsomes imbedded in, or sheathed by, linin) formed in the prophases of mitosis by transverse segmentation of the spireme thread, or which, in those cases where a continuous spireme is not formed, segregates as a separate element from the chro-

matin reticulum of the resting cell; the halving of each chromosome in metakinesis results in the formation of two daughter-elements, each of which has the value of a chromosome only in the daughter-cell in which it comes to lie; that is to say, metakinesis doubles the number of chromosomes. . . . The chromosome must be ascribed an actual value (in relation to the cell generation in which it occurs) irrespective of any prospective or retrospective value."

The body under consideration fulfills the conditions of the definition, and therefore should be classed with the chromosomes. It is to be hoped that we shall soon be in a position to give it a more exact status among these chromatin elements.



## ZOÖLOGICAL BULLETIN.

## A MALE ERPETOCYPRIS BARBATUS FORBES.

C. H. TURNER.

THE genus *Erpetocypris*, which was established by Messrs. Brady and Norman<sup>1</sup> in 1889, includes certain members of the old genus *Cypris*, which, owing to the fact that the natatory setae of the second antenna are non-plumose and do not reach beyond the tips of the terminal claws, do not swim but creep. Although females of about a dozen species of *Erpetocypris* are known, yet, to the best of my knowledge, no males of this genus have been either described or figured.

Recently, through the kindness of Mr. R. B. Randolph, of Seattle, Wash., I received a few specimens of *Erpetocypris barbatus* Forbes, which the donor had collected from a pond on the trunda near St. Michael, Alaska. This *Erpetocypris*, which was first described by Prof. S. A. Forbes<sup>2</sup> in 1893, is the largest American Ostracod known to science. Professor Forbes discovered it in Yellowstone Park, Wyoming; it has now been found by Mr. R. B. Randolph in the Yukon Valley, Alaska. Apparently all of Professor Forbes's specimens were females; the majority of those sent me by Mr. Randolph were males.

The shell of the male resembles that of the female both in shape and size; the male being 4.07 mm. long and 2.10 mm.

<sup>1</sup> Brady and Norman, "A Monograph on the Marine and Freshwater Ostracoda of the North Atlantic and of Northwestern Europe. Section I, Podocopa," *Sci. Trans. of the Roy. Dublin Soc.* Vol. v (ser. ii), 1889.

<sup>2</sup> Forbes, S. A., "A Preliminary Report on the Aquatic Invertebrate Fauna of Yellowstone National Park, Wyoming, and of the Flathead Region of Montana," *Bull. U. S. Fish Com. for 1891, 1893*, pp. 244-246; Pl. XXXVII, Figs. 3, 4; Pl. XXXVIII, Figs. 5-8.



high, while the female is 4.00 mm. long and 2.00 mm. high. But there are two respects in which the shell of the male differs



FIG. 1.

from that of the female: first, the shell of the female is opaque, or nearly so, but that of the male is so transparent that the testes and appendages may be seen through it; second, there are a few blotches on the outside of the female shell, but on the outer side of the large valves of the male shell, and attached to the dorsal margin of the same, there is a pair of smaller valves. It looks as though

the creature had partially sloughed one pair of valves, and then grown a larger pair beneath them. It is well known that certain Cladocera (*Ilyocryptus sordidus* Lievin) have this habit of partially sloughing the lorica and then growing a new one attached to the old; but, so far as I know, this is the first time that an Ostracod has been known to do so.

The first antennae of both male and female are alike; but the second antenna of the male, unlike that of the female, has a slender ultimate joint, and the three terminal claws arise from the penultimate segment (Fig. 1).

The first maxilla of the male is similar to that of the female, the two large claws being smooth; but, as usual among male Ostracods, the second maxillae of the male are modified for clasping. The structure of the male maxillae is illustrated in Fig. 2. Fig. 2 also shows the difference in size:

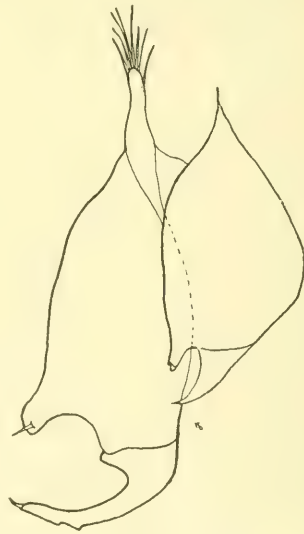


FIG. 2.

between the two male maxillae. The structure of the legs is practically the same in both male and female. The same may be said of the abdominal rami, although those of the male are a trifle longer and more sinuous than those of the female.

The copulatory organs, the structure of which is depicted in Fig. 3, are quite large, and, as usual in male Ostracods, of unequal size. The following table contains the dimensions of the copulatory organs of five different individuals.

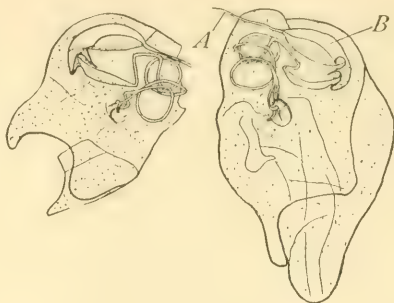


FIG. 3.

		1 mm.	2 mm.	3 mm.	4 mm.	5 mm.
Larger organ	Length	1.58	1.77	1.64	1.90	1.58
	Width	0.98	0.92	0.92	0.98	0.85
Smaller organ	Length	1.28	1.44	1.31	1.71	
	Width	0.85	0.85	0.92	1.05	

It will be seen at a glance that the ratio of the width to the length is much greater for the smaller than for the larger organ of the same individual.

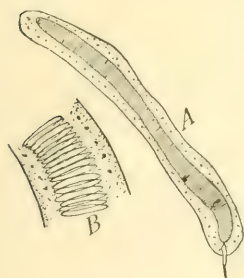


FIG. 4.

The vas deferens, shortly after entering the proximal end of the copulatory organ, forms an irregular enlargement (Fig. 3, B). After leaving the small distal end of this portion, the vas deferens coils into a loose knot before terminating, near the middle of the organ, in two or three tubes.

Zenker's organ (Fig. 4, A) is about nine times as long as wide, being 0.81 mm. long and 0.09 mm. wide. Its structure is simpler than the corresponding organ of any other Ostracod known to me. The central core is composed of a series of narrow rings, arranged one in front of the

other (Fig. 4, *B*), but neither spines nor other structures project outwards (laterad) from it to the wall of the capsule.

The testis lies within the wall of the shell and consists of four concentric, unequal-armed, *U*-shaped tubes, which lie above (dorsad of) the lateral diverticulum of the digestive tract. The shorter arm of the *U*, which is situated above (dorsad of) the long arm, is from one-third to one-half as long as the other arm. Each tube is broadest at the free end of the longer arm, from which extremity it gradually tapers to the free end of the shorter arm, where it terminates in a point. Judging from a half dozen specimens examined, the sperm mother-cells are confined to the smaller arm, and the crook which unites that arm to the longer limb of the *U*. Usually there is a pair of testes, one in each valve of the shell; but in one of the specimens examined there was a well-developed testis in one valve, but not even a trace of a testis in the other.

CLARK UNIVERSITY, SOUTH ATLANTA, GA.,  
December 24, 1898.

## THE REDUCING DIVISIONS IN THE SPERMATOGENESIS OF DESMOGNATHUS FUSCA.

B. F. KINGSBURY.

DESPITE the fact — perhaps rather because of it — that the spermatogenesis of salamanders was the first to receive a careful investigation, and has since been twice made the subject of rather monographic treatment, there exist at present considerable confusion and disagreement in the results of the different investigators.

Flemming,<sup>1</sup> in 1887, in his paper in which he recognized two divergent types of mitosis to which he attached considerable significance, the "heterotypic" and "homotypic," gave the following scheme of spermatogenesis in *Salamandra*: (1) a period of multiplication of the cells; (2) a period of growth in which are formed the spermatocytes (of the first generation), large cells; these, by a division proceeding generally, though not universally, according to the heterotypic plan, form daughter-cells of medium size; and these, by another division, generally homotypic, sometimes heterotypic, form small (granddaughter) cells which are directly transformed into the spermatozoa.

Vom Rath,<sup>2</sup> in 1893, followed with a paper upon the spermatogenesis of *Salamandra*, in which he added to the three generations of cells recognized by Flemming three others, in the last two of which occurred a reduction by means of tetrad formation, which, after the appearance of Flemming's work on *Salamandra*, had been already observed in several invertebrates, and by vom Rath<sup>3</sup> himself in the mole-cricket (*Gryllotalpa vulgaris*).

<sup>1</sup> Flemming, W., "Neue Beiträge zur Kenntniss der Zelle. I. Die Kerntheilung bei den Spermatocyten von *Salamandra maculosa*," *Arch. f. mikr. Anat.* Vol. xxix, p. 389. 1887.

<sup>2</sup> Vom Rath, O., "Beiträge zur Kenntniss der Spermatogenese von *Salamandra maculosa*," *Zeitschr. f. wiss. Zool.* Vol. lvii. 1893.

<sup>3</sup> Vom Rath, O., "Zur Kenntniss der Spermatogenese von *Gryllotalpa vulgaris*," *Arch. f. mikr. Anat.* Vol. xl, pp. 102-132. 1892.

*garis*); so that the way was well paved for the recognition of similar results in *Salamandra* as well.

Meves,<sup>1</sup> finally, after a careful reinvestigation of the spermatogenesis of *Salamandra*, has found that Flemming was right as to the number of cell generations, and vom Rath wrong; that there is no tetrad formation and no reduction in the Weismannian sense; both of the final divisions being equation divisions; the first heterotypic in character, the second homotypic — not mixed, as Flemming had thought.

The large number of forms in which tetrad formation or its equivalent has since been found to occur might suggest that vom Rath is nevertheless right, or partially right, and Meves wrong. My results, however, upon the American salamander *Desmognathus fusca* confirm Meves's interpretations in all the essential points; no tetrad formation occurs, unless exceptionally, and the two final divisions recognized by Flemming are both equation divisions. Though this is the case, there yet exists the possibility of a qualitative reduction, as will be indicated below.

After the last division of the spermatogonia there occurs a well-marked synapsis stage, such as has been recognized by Moore<sup>2</sup> in Elasmobranchs, in which the detailed structure of the nucleus becomes very difficult to make out. The chromatin emerges from the synapsis in the form of a fine, intricately coiled thread or threads (it has not yet been ascertained which), and the nucleus enters on its period of growth preparatory to the first of the two "reducing" divisions. During this period the chromatin thread (or threads) shortens and thickens, and finally may be resolved into twelve horseshoe-shaped loops, which, in most cases at least, are so arranged as to have their ends — the open side of the loop — opposite the centrosphere, with its centrosome, now precociously divided (Fig. 1).

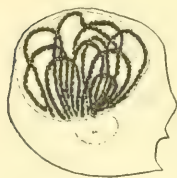


FIG. 1.

The division into which the nucleus is about to enter pro-

<sup>1</sup> Meves, Fr., "Ueber die Entwicklung der männlichen Geschlechtszellen bei *Salamandra maculosa*," *Arch. f. mikr. Anat.* Vol. xlviii, pp. 1-83. 1896.

<sup>2</sup> *Quart. Journ. Micr. Sci.* Vol. xxxviii, pp. 275. 1895-96.



ceeds according to the heterotypic plan, as both Flemming and Meves have already described in *Salamandra*. The twelve segments lose their position relative to the centrosphere, split longitudinally and incompletely (or, according to Meves, completely but with a subsequent fusion of their ends; I have not been able to determine this satisfactorily), and by a shortening and thickening become converted into rings, loops, or by twisting into 8's, as has been so often described and figured since the appearance of Flemming's paper in 1887. The split chromatin segments, in the form of rings or loops, generally more or less irregular, take up a peripheral position in the nucleus under the nuclear membrane. The centrosomes diverge within the centrosphere, the spindle is formed between them, in which the chromatin rings take up their position, forming the figure so characteristic of heterotypic mitosis. In the anaphase, as the daughter-chromosomes are passing to the poles, a second precocious, longitudinal splitting takes place, as recognized by Flemming. As the chromosomes approach the poles, however, they become so closely massed (possibly fused?) that it has been impossible to trace the continued existence of this splitting. In the telophase they become again separated from each other, still retaining their arrangement in relation to the pole (centrosome) (Fig. 2), the apices of the *V*'s all turned in the same direction.

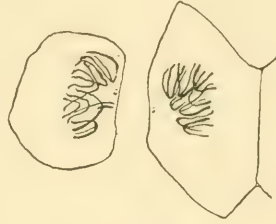


FIG. 2.



FIG. 3.

The nucleus of the spermatocyte of the second order does not go into a true resting stage, but the chromosomes remain distinct and easily distinguishable. Each loop is furthermore longitudinally split, so that there are twenty-four (presumably), which, however, are not entirely separate and independent, but are joined together in twos at the apices of the *V*'s (Fig. 3).

I believe these pairs are undoubtedly the incompletely split chromosomes of the anaphase in the previous division, although their close massing in the late anaphase has rendered it so far

impossible to trace them. The longitudinal splitting may have been complete, and the fusion of the apices been of secondary occurrence. The two chromatin segments so joined in pairs at their middle points show a tendency to diverge from each other, and in most cases, therefore, each pair is formed of four chromatin threads radiating from the point of fusion and lying in two planes at right angles to each other, as indicated in Fig. 4. There follow a shortening and thickening of the chromatin threads by which each pair becomes converted into a + or an X.

These usually tend to lie near the periphery of the nucleus under the nuclear membrane, as do the rings in the corresponding stage in the spermatocyte of the first order. Finally, the fusion is dissolved and there are formed from each + or X two V's, daughter-chromosomes of the second division. These



FIG. 4.

are generally quite irregularly distributed at first; soon, however, they take up their position in the center of the cell, to form a somewhat loose equatorial plate in which the daughter-chromosomes are generally quite widely separated from each other.

Migration to the two poles to form the nuclei of the spermatids occurs in *Desmognathus* in the manner already described by Flemming and Meves for *Salamandra*.

The early splitting and early and complete separation of the chromosomes in the spermatocyte of the second order was recognized by Flemming and made a characteristic of the peculiar form of mitosis which he called "homotypic," basing the type on the conditions found in the second division in *Salamandra*.

Although it seems to me probable that the X's and their dissolution into V-shaped chromosomes is due simply to an incomplete precocious longitudinal splitting of the chromosomes, which upon its final completion gives an equation division of the chromatin mass represented by the formula

$\frac{a-b}{a-b}$ , thus,  $\frac{a}{a} \frac{b}{b}$ , it is nevertheless possible that the final separation is represented by  $\frac{a-a}{b-b}$ , thus,  $\frac{a}{a} \frac{b}{b}$ ; and therefore it

would be a qualitative, reducing division in the sense of Weismann. No absolute decision between these two possibilities could be arrived at; nor does it seem to me likely that a determination of the way in which the separation actually occurs may be gained.

I know of no results on other forms that furnish circumstantial evidence in favor of a qualitative reduction taking place in the manner suggested above as possible. Meves, it should be remembered, found that in *Salamandra* the second division was a qualitative equation division, and did not describe anything corresponding to the X formation that occurs in *Desmognathus*.


The union of chromosomes, or daughter-chromosomes, in pairs, whether with a reduction of the number one-half or not, is conceded by most as furnishing a basis for a qualitative reduction. Typically (perhaps) the reduction is accomplished by the union in pairs of the chromosomes before the first splitting; there being a reduction of the number to one-half and a second longitudinal splitting being wanting; or (Calkins<sup>1</sup> in *Lumbricus*) conjugation may take place after the first longitudinal splitting, and reduction follow, as in the typical case. According to Lee,<sup>2</sup> in *Helix* a longitudinal splitting of the chromosomes, separation of the daughter-chromosomes, and a subsequent fusion (so far resembling Korschelt's<sup>3</sup> results on *Ophryotrocha*) take place before the divisions of the spermatocyte, of which the first is longitudinal, the second transverse; there is thus no reduction in the number of the chromosomes, but there is a quantitative and qualitative reduction in the second division, the latter depending on the heterogeneous conjugation of chromosomes before the first division.


If the second division in *Desmognathus* is to be looked upon as a "reducing" division, it may be considered in two ways. The original union of the chromosomes, after two longitudinal splittings of the united chromosomes, is dissolved and a new union between the daughter-chromosomes established; or,



<sup>1</sup> *Journ. Morph.* Vol. xi, pp. 271-302. 1895.

<sup>2</sup> *La Cellule.* Vol. xiii, pp. 201-270. 1897.

<sup>3</sup> *Zeitschr. f. wiss. Zool.* Vol. lx, pp. 543-688. 1895.

from the standpoint of the more typical mode of reduction by tetrad formation with longitudinal and transverse divisions, there would occur in *Desmognathus* a reduction in number to one-half, a longitudinal (equation) division, followed by an attempt at a second longitudinal division, which, however, is not completed, and is prevented from being completed, by the second division, which is transverse. Shorten the interval elapsing between the first and  second divisions, and (possibly thereby) eliminate the second longitudinal splitting, and the process is reduced to the typical form.

 It seems to the writer, however, far more likely that both divisions in *Desmognathus* are equation divisions, in agreement with the results of Brauer, Hertwig, Moore, Meves, and the majority of the botanical workers.

There are two or three interesting comparisons that may be made between the first and second divisions of the spermatocyte. In the period of growth to form the spermatocyte of the first order the chromatin segments form loops or *U*'s with the open end toward the centrosphere and centrosome (Fig. 1). In the spermatocyte of the second order, on the other hand, the apices of the *V*'s are toward the centrosome. In the longitudinal division of the segments in the spermatocyte of the first order the free ends of the segments remain united (or fuse after separating), forming rings. In the spermatocyte II the apices (opposite ends of the  joined chromosomes) remain united, and the corresponding figure in the second division is a cross. The chromatin in the two divisions is thus contrasted in  these two particulars, to which it is felt some importance may attach.

In *Desmognathus*, therefore, there are two divisions intervening between the last spermatogone division (as so determined) and the spermatid, in both of which occurs longitudinal split-

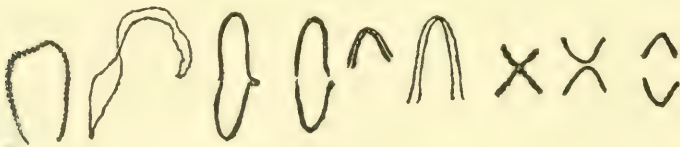


FIG. 5

ting of the chromatin segments, there being thus agreement with the results of Flemming and Meves on the European form *Salamandra*, as opposed to those of vom Rath. The possibility of a reducing division is nevertheless believed to exist. The diagram on the preceding page sets forth the author's interpretation of the division of the chromosomes in the last two divisions.

CORNELL UNIVERSITY, ITHACA, N. Y.,  
February 1, 1899.







## OVARIAN STRUCTURE IN AN ABNORMAL PIGEON.

MICHAEL F. GUYER.

IN the course of my studies on the spermatogenesis and ovogenesis of the pigeon, a peculiar abnormal case came into notice which seems deserving of special mention because of its comparative isolation from the main subject, as well as for certain very interesting features it presents. The case was that of a dove which showed many unusual traits. Her actions and general appearance were very singular, and an anatomical examination revealed in the ovary a structural difference from the common type.

Whether the bird exhibited true arrhenoidy, — the female taking on the external characteristics of the male, — as described and named by Brandt ('89), is rather hard to determine, because the male and female doves are not to be distinguished ordinarily by means of their plumage. The abnormalities in the structure of the ovary, however, seem to be of much the same nature as he described for such conditions. Willey ('91) reports a somewhat similar case in the domestic duck.

The dove was a white bird with a faint yellowish ring around the back of her neck. She came into my possession through the kindness of Dr. Watasé, who raised her from a pair which he obtained originally in 1897 from the collection of Professor Whitman.

To Professor Whitman I am indebted for the following account of her genealogy. Very generously he has also supplied me largely with the material for the research upon the spermatogenesis of hybrids and of normal pigeons, in which I am at present engaged, and my obligations to him are very great.

The original ancestors of the dove in question were an ordinary ringdove (*Turtur risorius*) and a Vienna white (*Columba*

*alba*). Most authorities place the latter form in the same species as the former. The immediate progeny of the pair just mentioned was always brown in color, the male being generally of a slightly lighter shade than the female.

When these doves of the second generation bred they brought forth young which seemed usually to revert to the ancestral type; one member of the resulting pair was generally white, and the other brown. Curiously enough, out of some eighteen birds of this generation that I killed, the brown ones.

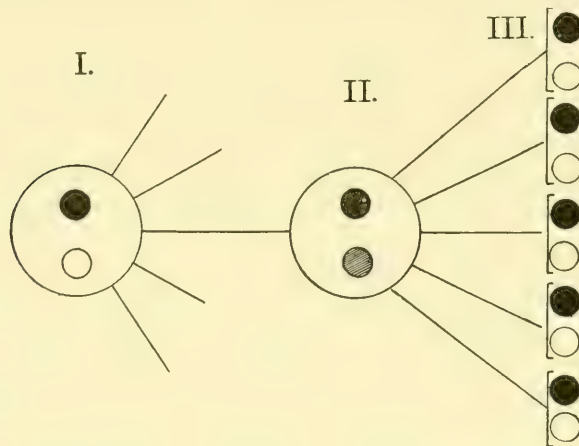


FIG. 1.—A diagram showing the lineage of the dove under discussion.

were invariably male and the white ones female. In one case where both of the young birds were brown, they were male, and in another where they were white, both were female.

Schematically, the lineage may be represented as in Fig. 1. The ancestral pair, one brown and one white, are represented by the two enclosed circles to the left. They give rise to a number of offspring, one pair of which is indicated by the two enclosed dark circles to the right of the first. These, breeding again, bring forth a large number of pairs, of which one member in each pair is usually white, the other one brown. The bird under discussion was of this last or third generation.

From the beginning she seemed to be abnormal. She was always of a very nervous disposition, and would fly wildly about when her cage was approached. While under observation she

was continually shivering and trembling. The same was true when a mate was placed in her cage. Although a number of different mates were placed with her at various times, she remained sterile. She was about two years old when killed and had never laid an egg.

In general appearance she was a very disreputable looking fowl. Her plumage was always ruffled and disordered, the large feathers of the tail being especially ragged and rough looking. Her voice resembled that of neither the ordinary male nor female, but was a sort of curious little crow, unlike anything I had ever heard. One eye was abnormal and gave her an odd, staring look.

Upon dissection the ovary from a general view seemed normal, but when sectioned and examined under the microscope many peculiarities of structure were discernible.

There were very few of what could be called normal eggs. The abnormalities were of several kinds, but a given type was generally more or less localized. The eggs varied in size, from small ones just visible under the low power of the microscope, to those measuring a fraction over a millimeter in diameter.

The first peculiarity to strike the attention was the large number of double eggs; that is, two eggs lying within one follicle (Figs. 2, 3, and 4). Sometimes the follicle was absent wholly or in part, but in such cases the relation was yet so close as to be easily distinguishable. Often no intervening membrane was present between the two eggs, and the appearance was that of an egg cell containing two nuclei (Fig. 9). In places three and even four eggs were to be seen within a common follicle. In general, the multiple eggs seemed to lie in colonies; that is, where one case occurred, a number were

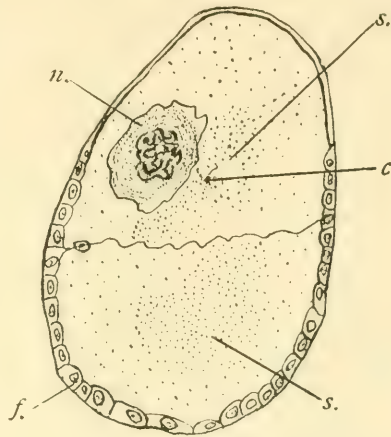


FIG. 2.— $\times 370$ . A double egg showing one nucleus and centrosome. The follicle cells are absent on one side. *c*, centrosome; *f*, follicle; *n*, nucleus; *s*, sphere.

usually to be found in the same vicinity. As high as sixteen pairs, and two instances of triple eggs, were counted in the field at one time under a magnification of 110 diameters. This is, of course, an exceptional condition. Commonly four or five

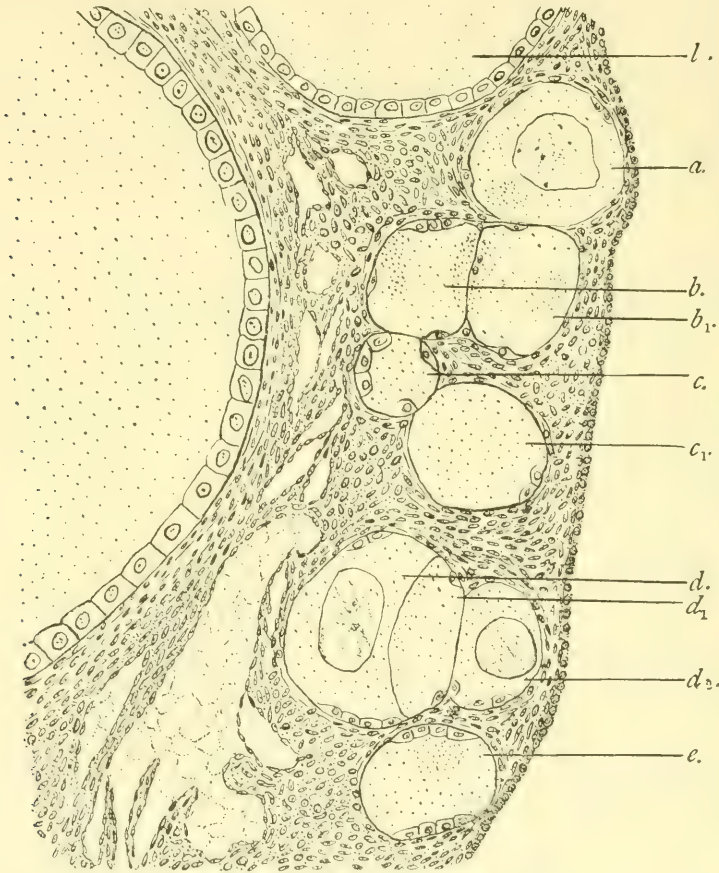


FIG. 3.— $\times 370$ . A section of part of the ovary. Every egg in the field is a multiple form;  $b$ ,  $b_1$ ,  $c$ ,  $c_1$ , is a connected group of four;  $l$ , the edge of a large egg.

pairs are the most to be seen. Fig. 3 shows a section of a part of the ovary magnified 370 diameters. By following out the serial sections, the relations of the eggs represented in the figure were determined. Examining them in such a manner,  $a$  (Fig. 3) was found to be double;  $b$  and  $b_1$  formed a double, likewise  $c$  and  $c_1$ ;  $b$  and  $c$  were also connected as doubles. Thus



the group,  $b, b_1, c, c_1$ , really formed a cluster of four. The next group,  $d, d_1, d_2$ , formed a set of three, and the last egg,  $e$ , was double.

Almost all gradations of union between the two related eggs could be seen. In some cases there seemed to be but one mass of cytoplasm containing two nuclei (Fig. 9); in others a dividing membrane was present, but was incomplete. In still other examples there was a distinct membrane between the eggs, together with a few strands of connective tissue, with the follicle cells at the edges apparently creeping gradually in along the line of demarcation. Occasionally scattering follicle cells were found between the two eggs.

Most of the double forms were of small diameters. When large eggs were doubled they seemed to be in a state of degeneration. They contained large vacuoles, and, perhaps, in addition the cytoplasm was being consumed by phagocytic action. Fig. 4 represents four sections taken in order at varied places from one of the larger double eggs. At *A* (Fig. 4), in one of the eggs, the nucleus is shown. It is considerably shrunken. A faintly marked cell wall separating the two eggs is visible, and lining it on either side is the material of the so-called attraction sphere or yolk nucleus ( $s$ ). The follicle cells at one edge ( $f$ ) have lost their walls and form a sort of syncytial mass. At *B* (Fig. 4) the section shows the membrane which separates the two eggs as still visible. The nucleus of the other egg has come into view and is also much shrunken. At this point the sphere substance is seen to project out more toward the center of the upper egg, and in the center of this mass a clear space or vacuole ( $v$ ) is visible. As the sections are passed over, this vacuole rapidly becomes larger and appears as at *C* and *D* respectively. In *C* there is no trace of a dividing cell wall, and the cytoplasm of the two cells mingles. In the sphere substance of the lower cell a second vacuole has made its appearance, and it gradually merges into the first, as seen in *D*.

The formation of vacuoles is very common, especially in the larger eggs, both single and double. In some of the eggs, indeed, most of the cytoplasm has disappeared, and only a large vacuole remains. Vacuolation begins invariably in the sphere

substance. Fig. 5 shows vacuolation just commencing in a large single egg.

The sphere substance in both single and double eggs may be found in various conditions. In many places it seems to be

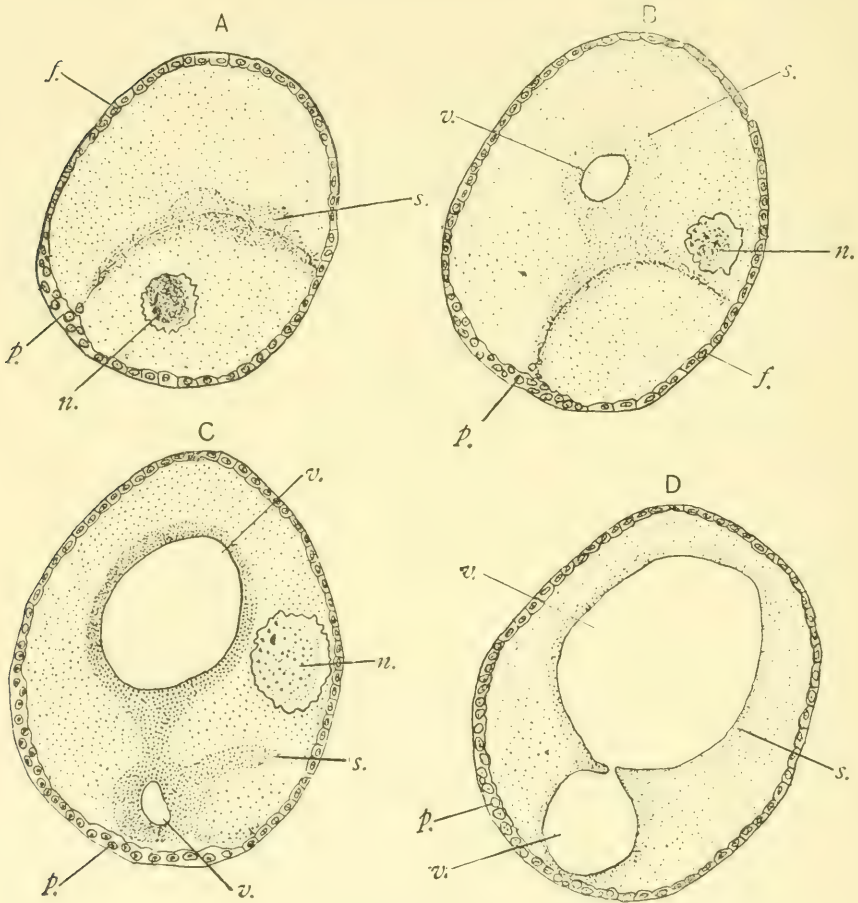


FIG. 4. —  $\times 110$ . Four sections of a series from a large vacuolated double egg. *f*, follicle; *n*, nucleus; *p*, phagocytes; *s*, sphere; *v*, vacuole.

deteriorating. Besides being connected with the formation of vacuoles, it seems to play some rôle in the formation or dissolution, as the case may be, of the cell wall in double eggs. It is always in contact with the intervening cell membrane (Figs. 2 and 4, *s*). In the eggs of normal pigeons it remains in more or

less of a single mass, but here it may often be seen scattered throughout the cell in little clumps. These often seem to melt together, as it were, and form deeply staining liquid-like masses.

The nuclei in many of the eggs were shrunk, and showed an irregular wavy border. This was true of the larger eggs almost without exception. Fig. 5 shows a common form. The nuclear material is collected into a granular mass in the center. Irregular rods and granules of chromatin material can be dis-

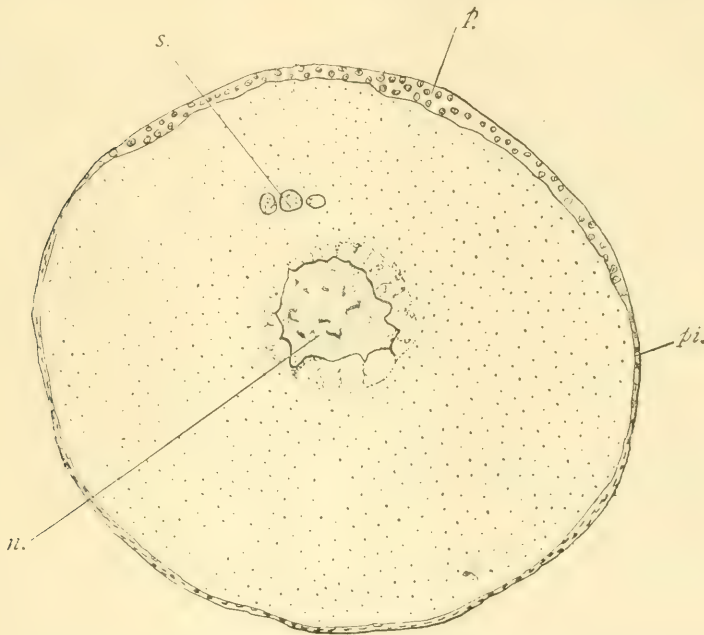


FIG. 5. —  $\times 78$ . A large egg showing phagocytes (*p*) at the periphery on one side, and pigment (*pi*) on the other. The nucleus (*n*) is shrunk and the sphere (*s*) forming vacuoles.

tinguished. The nuclear membrane is collapsed and shrunk, and surrounded by a lighter area of cytoplasm, which has the appearance of streaming or being drawn toward the nucleus. This aspect is due probably to the contraction of the nucleus, which carries in the surrounding cytoplasm as it recedes. In other cases the nuclei seemed to be in the last stages of degeneration, and were simply clear areas crossed by colorless feathery strands (Fig. 8).

Nucleoli might or might not be present. In the normal egg

they are very characteristic deeply staining round bodies. In the abnormal form, if present, they were generally small and irregular. Occasionally they appeared as pale, uneven masses, which seemed to be disintegrating.

Centrosomes were frequently present, and were always closely connected with the sphere substance. In none of the eggs was mitotic division found in progress. Fig. 6 shows two centrosomes (*c*) lying side by side in the midst of a system of radiating fibers. The sphere substance is

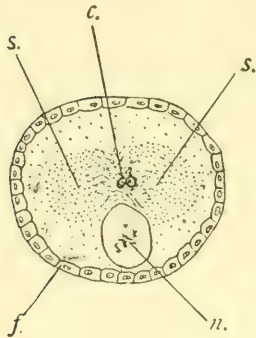


FIG. 6.— $\times 135$ . An egg showing two centrosomes (*c*). *f*, follicle; *n*, nucleus; *s*, sphere.

collected for the most part into two more or less crescentic areas at either side. The centrosomes proper were surrounded each by a small clear space, and then by a darker area of what appeared to be sphere substance. Outside this latter region came the system of fibers. The nucleus had the characteristic shrunken appearance. Another egg was found in which two centrosomes, each surrounded by a mass of sphere substance, were lying on either

side of the nucleus, but no trace of a spindle or other preparation for mitosis was visible. In Fig. 2 a single centrosome (*c*) is seen.

Another common phenomenon shown by many of the eggs was the destruction of the cytoplasm by means of phagocytes or eating cells. There were two methods of consumption by such cells. Either they wandered into the interior of the cell and gradually devoured the material about them, or they multiplied around the periphery of the egg and gradually crowded in upon the cytoplasm, consuming it as they approached the center. The first method was rare, being seen in only three or four eggs, and then to a limited extent. This is unlike the cases described by Brandt ('89) and Willey ('91), where this type of yolk resorption seemed to be common (*cf.* Brandt, '89, Figs. 5-8; also Willey, '91, Figs. 1 and 2).

The second process was the usual one. There were scarcely any of the larger eggs that did not display it to a greater or less



extent. Fig. 7 shows a somewhat advanced stage. The section is to one side of the center of the egg. The remaining cytoplasmic material (*cy*) exhibits a very ragged, irregular border, surrounded by numerous nuclei lying in one continuous mass of cytoplasm. These nuclei are the nuclei of the erstwhile follicle cells, whose walls have disappeared, and the cell contents flown together to form a syncytium. Brandt pictures a very similar phenomenon in his paper (*cf.* Brandt, '89, Figs. 4, 13, and 16).

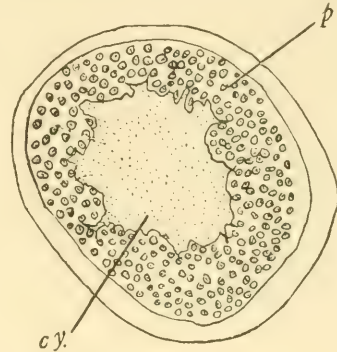


FIG. 7.— $\times 110$ . An egg in process of resorption by means of the transformed follicle cells. *p*, phagocytes; *cy*, cytoplasm.

In regard to the origin of the phagocytes in such cases there is some difference of opinion. Brandt ('89) describes the occurrence as due to the wandering in of follicle cells, while Willey ('91) maintains that in the case he studied, the cells were transformed stroma cells. Ruge ('89) says that, in such cases of resorption in the amphibian ovary, both the follicle and stroma cells, or white blood corpuscles, play a rôle.

In the present instance the process is carried on almost wholly by the transformed follicle cells. In a very few cases where eggs lay in the neighborhood of the larger blood vessels, cells from the outside seemed to be wandering through the follicular layer; but they could never be traced into the interior of the egg. At that part of the egg periphery not yet attacked by the eating cells, normally, the follicle is visible as a comparatively thin layer of cells, each with a distinct membrane. When about to undergo the transformation into phagocytes they enlarge, the cytoplasm shows a different micro-chemical reaction, and the cell boundaries become less distinct. At a little later period many of the cells are seen undergoing karyokinetic division. After karyokinesis, they lose their walls and are ready to take on the new function of resorption.

Often, as is shown in Fig. 5, the new cells (*p*) were confined to one side of the egg, and resorption occurred only from that



side. On the opposite side, in the figure, the follicular cells have entirely disappeared, leaving behind a more or less distinct layer of pigment (*pi*). Under such conditions the phagocytes continue to advance until they pass entirely across the egg, devouring the cytoplasm as they go.

Where the cell contents yet remained intact in the larger eggs, it always had a peculiar, finely granular, homogeneous appearance, very different from that of the same sized egg of a normal bird. In the latter egg the cytoplasm always has a reticulated appearance, and grows much denser as it approaches the periphery. Oil droplets of varying size are scattered plentifully throughout it. No trace of such structures was evident in the eggs under discussion.

The question arises whether the doubling of eggs is really a division of the original primordial ovum, or whether it may not be a fusion of two cells, due to the general deterioration manifested everywhere throughout the ovary. I had scarcely completed the observations here recorded, when I came upon the paper of Stoeckel ('99), and found in his plates certain figures which agreed almost identically with some of my own preparations. His drawings were made from sections of the ovary of a woman, and show the same curious doubling of cells and nuclei here mentioned (*cf.* Stoeckel, '99, Figs. 2-15). He is inclined to regard the doubling as due to a division of the primordial egg. He also records the case of an embryonic infant in which such double eggs and nuclei were very common and apparently perfectly natural phenomena. In regard to the child he says that doubling is unquestionably due to an amitotic division of the egg, or, in his own words: "Diese Befunde zeigen zunächst, dass eine direkte Ei- und Follikeltheilung im fötalen Ovarium sicher stattfindet." (Stoeckel, '99, p. 370.)

His first case, however, was that of an adult, a nullipara, twenty-nine years of age. From the facts he mentions in regard to her, it does not seem improbable that the phenomena of double egg formation, as in the dove, was a pathological one. Her history showed that she was of weak constitution and chlorotic.

As to the doubling of eggs in the dove ovary, I am inclined

to believe that such conditions are brought about by both division and fusion. The greatest amount of doubling was seen in the very young ova, and, I think, resulted generally from division. Although no actual division was observed, yet the general appearance of the cytoplasm, and the plump, full nuclei of the young double eggs, exhibited none of the signs of deterioration one would expect if a fusion of two eggs, preparatory to going to pieces, were in progress. Some of the smaller eggs are doubtful, however, and the indications are that there may be fusion instead of division. There can be but little doubt that a form, such as is shown in Fig. 8, is the result of a fusion.

By following out the serial sections, it was found to be really two ova with a single nucleus which resulted from the fusion of the two original nuclei. The nucleus thus formed seemed to be almost completely degenerated, and was wholly devoid of

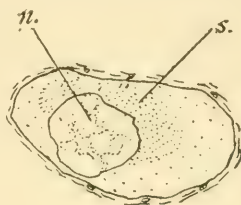


FIG. 8. —  $\times 525$ . A double egg formed by fusion. The two nuclei have united to form one. The follicle has disappeared. *n*, nucleus; *s*, sphere.

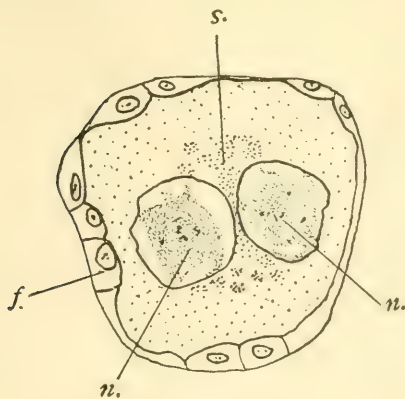


FIG. 9.

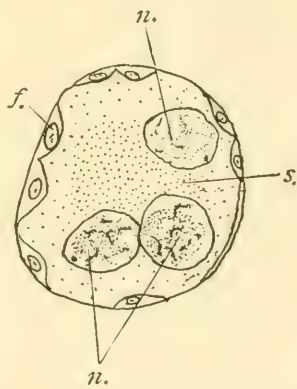


FIG. 10.

FIG. 9. —  $\times 525$ . A double nucleated cell. *f*, follicle; *n*, nucleus; *s*, sphere.

FIG. 10. —  $\times 525$ . A triple nucleated cell.

contents beyond a few rough, straggling threads of poorly staining material. The follicle had disappeared. Figs. 9 and 10 are two rather doubtful cases. In each the follicle was represented by a few large cells irregularly disposed, but whether

the follicle was disappearing or forming could not be determined. In Fig. 9 the nuclei are somewhat shrunken and consist principally of a granular mass. The sphere substance, which, as was above mentioned, seemed always in some way connected with the formation or disappearance of the separating membrane, lies between the nuclei and is broken up into granular clumps. In Fig. 10, an egg with three nuclei, the sphere seems to be perfectly normal. Two of the nuclei lie in contact and seem to have recently divided. The third lies apart and contains only a few feathery strands of material, which seems to be breaking up and disappearing.

In some of the larger ova, as in Fig. 4, where vacuoles have appeared, or where cytoplasm is being devoured by the transformed follicle cells, the process is probably one of fusion preparatory to disintegration. It is not improbable that in some instances the two cells were a product of the same division, and after lying side by side and passing through a period of growth, they again fused into one mass as degeneration set in.

Regarding the cause of such abnormalities as have been described, but little can be said. Whether the abnormal structure of the ovary is due to the derangement of other organs of the body, or whether the accompanying bodily peculiarities are caused by the unnatural ovary, cannot be definitely determined. One would, however, without evidence to the contrary, naturally incline towards the latter view. The far-reaching effect of a change in the reproductive organs, especially in case of injury or removal, is well known to all. Yet it is not impossible that some stimulus from outside the ovary, perhaps of a chemical nature, could act upon it secondarily and produce the modifications described. The blood would provide a ready means for the conveyance of any chemical substance that might be formed elsewhere in the body. Cases are not unknown where division of the unfertilized ovum has been brought about by means of chemical stimulus. Interesting suggestions arise, too, that these phenomena might in some way be connected with hybridization, and, indeed, certain facts have come to light recently in my study of hybrid material, which render this idea by no

means unpalatable. The subject is at least deserving of very careful consideration.

The principal facts adduced in this paper are briefly as follows :

(1) A dove, the offspring of a Vienna white (*Columba alba*) and a common ringdove (*Turtur risorius*), remarkable for her unusual appearance and manner, was found, upon dissection, to have an abnormal ovary ;

(2) The ovary contained many double eggs, that is, two or more eggs lay within one follicle ; they might or might not be separated by a distinct membrane ;

(3) Nearly all of the larger eggs were vacuolated ;

(4) The vacuoles always appeared in connection with the substance of the attraction sphere ;

(5) The membrane separating double eggs also seemed to be related in some way to the sphere ;

(6) The nuclei, especially of the larger eggs, were generally shrunken and seemed to be degenerating ;

(7) Nucleoli were frequently present, but in many cases were indistinct and irregular in outline ;

(8) Centrosomes were frequently present, but mitotic division of the eggs was never observed ;

(9) Many of the eggs, especially the larger ones, were undergoing resorption by means of phagocytes, which in the vast majority of cases, if not all, were transformed follicle cells ;

(10) Instances were found where the follicle cells had disappeared along part of the periphery of the egg, leaving behind a deposit of pigment. In such cases one side of the egg was usually undergoing dissolution through the activity of the phagocytes ;

(11) The doubling of eggs seemed to be due in most of the smaller eggs to (a) a division of the primordial cell, and in the larger ones to (b) a fusion of contiguous cells ;

(12) The cause of such abnormalities is not known. Possibly some connection with hybridization may be shown later.

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## SOME INTERESTING EGG MONSTROSITIES.

CHARLES W. HARGITT.

UNDER the caption "Ein Ei im Ei" there appeared in the *Zoologischer Anzeiger* of Aug. 17, 1896, an interesting account by Vom Seigm. Schumacher of a small egg of the fowl enclosed within a larger. This report has recalled my attention to observations made by myself some years ago and reported to the Indiana Academy of Science, but which were never published except by title. Similar cases of somewhat similar character which have since come to my knowledge, and their somewhat unusual and abnormal phenomena, lead me to submit the following statement of facts which in their way may not be without a measure of interest.

The first case which came under my observation was an egg of very large dimensions, almost three inches long by about two inches in short diameter, brought into my laboratory by a student. It was a double egg in a rather unusual sense. The

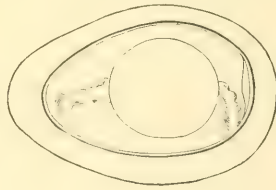


FIG. 1.

outer one was of the dimensions indicated, while the inner was of about normal size and form, and of perfectly normal structure. That is, it was composed of yolk, albumen, chalaza, shell-membrane, and shell. The outer was similar, except that it was wholly devoid of yolk. There was the usual proportion of albumen of the usual consistency, a shell-membrane, and a perfectly formed shell of the usual density. Fig. 1 presents a sectional view of the egg.

Considerable inquiry failed for some time to elicit any information of similar cases. Later a report was made by Mr. Charles Dury, of the Cincinnati Society of Natural History, of a somewhat similar case of a monstrous egg laid by an ostrich in the Cincinnati Zoölogical Garden. Of the exact size of this egg no data were given. Its similarity consisted chiefly in the fact that the center of the monstrosity was a normal egg. About this, as a sort of nucleus, there had been formed some twenty concentric layers of what the report simply indicated as a sort of tough, leathery-like substance, but which, I infer, was probably a toughened albuminous mass. Whether the whole was enclosed within a second shell the report did not designate.

Another case was brought to my attention by Prof. O. P. Jenkins, at that time of DePauw University, later of Stanford University. It was apparently of the same general character as the first one referred to. The same observer also gave me the record of a similar egg laid by a turkey-hen. In this case the egg was, as in the former, larger than the normal, and contained an inner one of somewhat smaller than normal dimensions. They were similar in all essentials, though with this difference: that while the outer shell was colored the usual way of turkey eggs the inner shell was pure white, thus giving rise to the remark of the one first reporting it, "that it was a turkey's egg with a hen's egg inside of it."

Among several other cases of a similar character which have come within my observation one has some features of peculiar interest. It was reported to me by Prof. Charles H. Gilbert, of Stanford University, who, though he did not personally see the egg, vouched for the substantial accuracy of the facts. The egg was taken from the nest almost immediately after its deposit, and was of the unusual size of those already designated. Like those, it was of the same double character throughout. But the matter of special interest was in the fact that within the inner was an embryo chick of considerable development. A letter from Professor Gilbert on the subject contains this account: "From the manner in which the details were given to me, I have no doubt that it was a *bona fide* case, and that

the embryo was developed at least as far in this perfectly fresh egg as would under ordinary circumstances occur on the fourth day of incubation."

One of the most recent cases of egg monstrosity came into my hands within a few months, and is in some respects wholly unlike any of the others. It consisted of two eggs, as shown in Fig. 2, partly independent, but united by a narrow connective (*c*), in the figure. They differed in size about as indicated, and presented the smaller ends toward each other—a fact in itself somewhat abnormal, as will be shown later. These eggs were devoid of hardened shells, but the larger had considerable deposition of calcareous matter over the entire membrane.

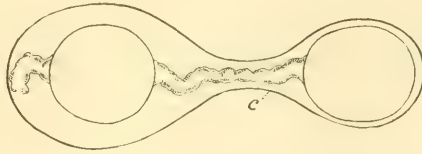


FIG. 2.

This was almost wholly lacking in the smaller. Upon opening the eggs, both were found to contain normal yolks of normal size, and each with distinct germinal areas. The interior of the yolks was of characteristic and normal composition. The different sizes of the eggs were due to the fact that while the larger had its usual amount of albuminous deposit, the smaller was almost wholly devoid of this. But while differing in the amounts of albumen it was in each of the same character, including the chalazal portion, which at the smaller ends communicated through the hollow connective, as shown in the sectional view of Fig. 2. The sizes of the eggs were as follows:

Total length of the two, 113 mm.; length of large egg, 55 mm.; length of smaller, 52 mm.; length of connective, 16 mm.; short diameter of larger, 40 mm.; short diameter of smaller, 23 mm.; short diameter of connective, 8 mm.

Concerning the origin of these abnormal eggs the views expressed by Schumacher are quite similar in most respects to those expressed in my original report. There seems little doubt that they have been produced by an unusual retention

of the egg within the uterus and by its recession through the oviduct over the regions of the albumen and shell glands. This might be effected without serious difficulty by a strong antiperistaltic action of the oviduct, to use Schumacher's phrase.

As a motive for such retention I have suggested the probability of some unnatural conditions, such as fright, confinement, etc. In the case of the ostrich referred to, this would seem plausible, and in some of the cases coming under my own notice, where the fowls had been confined within coops, such might be a most likely cause. The unusually artificial conditions of the ostrich might operate as a more or less permanent obstacle to the egg-laying. That the egg in this case had been retained for a considerable time within the uterine duct must be evident, and if the several layers were of albuminous secretion they could only have been deposited by successively passing over these glands.

Concerning the egg in which development of the embryo had gone forward as indicated, a similar process must have obtained, as is evident both from the state of development attained, as well as the second deposit of albumen and shell. It may not be without plausibility that by some such process arose the ovoviviparous habit common in many egg-laying animals. If an egg may go forward in development for four or five days under such conditions, why might it not be gradually extended until chicks might be born instead of hatched?

Concerning the egg shown in Fig. 2, it is obvious that a different account must be given. The most obvious explanation would seem to be that two eggs had been discharged from the ovary within brief intervals, but not coincident, since we should then have the not unusual phenomenon of a double-yolk egg, yet so closely following each other that they became connected by the albuminous secretions which would thus be continuous. The first to descend would thus receive its full complement of albumen, while the second would be scantily supplied owing to the depleted condition of the glands following the first discharge. But it will be noticed that by this account we should have the first egg descending the oviduct broad end foremost,

while ordinarily the opposite is the case.<sup>1</sup> That there is no insuperable difficulty in the matter, however, and that such is not invariably the case, I think is evident. I have discovered during these observations several cases in which normal eggs have shown evidence of such reversed descent, having upon the small ends of the egg-shell a vermian-like coil of indurated shell substance, apparently produced as a sort of concluding deposit from the shell glands strung out upon the descending egg.

SYRACUSE UNIVERSITY, December, 1897.

Since the above was in type a similar case in some respects was submitted by Prof. F. H. Herrick before the Morphological Society, an abstract of which appeared in *Science* of March 10, 1899. The rather distinctive feature of this was that the small, or inner, egg was included within the yolk of the larger. This would seem quite unusual, so far as my own inquiries have gone, at any rate, and would hardly be open to a similar explanation.

C. W. H.

<sup>1</sup> Foster and Balfour, *Embryology*, p. 17.





# A REDESCRIPTION OF *PARIOTICHUS* *INCISIVUS* COPE.

E. C. CASE.

AN unusually perfect specimen of this genus and species in the paleontological collection of the University of Chicago makes it possible to complete the description of the species, hitherto known only from a fragmentary skull, and to add some points to the characters of the genus, also known largely from the skull.

The family *Pariotichidae* was established by Cope in 1883 (3). He says (p. 631) "*Pariotichus* and *Pantylus* and probably *Ectocynodon* must be referred to a special family, the *Pariotichidae*, which has teeth like the *Edaphosauridae* but differs from it in the entire over-roofing of the temporal fossae." There is no mention here of the family belonging to the order *Cotylosauria*, but this is evidently the position in which he would have placed it, as it is regarded always in later writings as belonging in that order or suborder, as he then regarded it.

In 1895 he gave a tabular statement of the characters of the families in the order *Cotylosauria* (4):

## I. Teeth in a single series.

Teeth not transversely expanded; vertebral centra with surfaces only ossified; no hyposphen. . .	<i>Elginiidae.</i>
Teeth not transversely expanded; vertebral centra ossified; no hyposphen. . . . .	<i>Pariasauridae.</i>
Teeth with the crowns transverse to the axis of the jaws; vertebrae ossified and with a hyposphen-hypantrum articulation. . . . .	<i>Diadectidae.</i>

## II. Teeth in more than one series in (one or) both jaws.

Teeth with cylindric roots; vertebrae ossified. . .	<i>Pariotichidae.</i>
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In 1878 (1) the genus *Pariotichus* was described (p. 508): "The temporal fossae were covered by a roof continuous with

the postorbital region; the zygomatic arch extends low down, producing a resemblance to certain tortoises. The orbits are small and lateral, and the muzzle is short, with terminal nares. Their exact character cannot be ascertained. The teeth are rooted, and have compressed obtuse crowns with cutting edge; they diminish in length posteriorly, and do not display any elongate canine. The cranial bones do not exhibit any sculpture." In 1883 (3) (p. 631) this last statement was corrected: "The surface of the cranium has been mostly weathered away in the type of *Pariotichus*, *P. brachyops*, and I suspect that it is really sculptured and not smooth, as I originally stated."

In 1895 (4) an analytical table of the genera of the *Pariotichidae* was given. In this table the genus *Ectocynodon* is united with *Pariotichus*:

I. External nostrils lateral.

a. Palatal and splenial teeth with compressed crowns.

Teeth equal, acute. . . . . *Isodectes* Cope.

Teeth increasing gradually in length anteriorly. *Captorhinus* Cope.

Teeth enlarged on the middle of the maxillary and anterior part of the incisive series. . . . *Pariotichus* Cope.

aa. Palatal and splenial teeth obtuse, forming a grinding pavement.

Median maxillary and anterior incisor teeth enlarged. . . . . *Pantylus* Cope.

II. External nostrils inferior.

Mouth posterior in position, mandible short, and with a few acute teeth. . . . . *Hypopnous* Cope.

It is probable that *Helodectes* Cope pertains to this family.

In the same article (p. 443) there is given a more extended description of the genus *Pariotichus*. "The maxillary teeth display the enlarged median tooth characteristic of the species referred to *Ectocynodon*, although it is less prominent than in some of the latter, and it is probable that the premaxillaries display corresponding enlargement. The type of *Ectocynodon* (*E. ordinatus* Cope) is in the same condition as regards teeth of the premaxillary series, but a long tooth is present near the

mandibular symphysis, so that the characters are so far those of the other species referred here. The elongation of the maxillary tooth is more conspicuous than in the *P. brachyops*. In general this tooth is not absolutely very large, but the teeth anterior and posterior to it are small or very small. Besides the usual series of teeth on the maxillary bone, there are two or more series adjacent. In like manner on the mandible, beside the dentary series, there are two or three series, perhaps on the splenial bone, standing on a ledge on the same horizontal plane as the tooth-bearing edge of the dentary. In this genus, and probably in all the members of the family, the palate is roofed over posteriorly by the palatine bones. The pterygoids diverge early from the presphenoid region toward the zygomatic border, as in *Batrachia* generally. The mandibular articular surface consists of two cotyli placed transversely. The os tabulare is small, and is situated, as in other genera of the family, near the posterior junction of the supramastoid and supratemporal. The supraoccipital forms a narrow strip of the posterior border of the superior plane of the skull. The arrangement of the cranial bones is as I have described in the genera *Isodectes* and *Pantylus*, except that the prefrontal and postfrontal bones scarcely meet over the orbit, instead of separating the orbital border from the frontal. The occipital condyle, as in *Empedias*, is prominent, and has a median fossa.

"In *Pariotichus aguti* the vomers are elongate posteriorly and the palatines send an acute anterior process between them. The palatines are separated by a fissure which is narrow anteriorly and becomes wider posteriorly. Each interior border bears on its posterior two-thirds a row of small teeth. In this respect this genus differs from *Empedias*, where the palatines are closely appressed on the middle line. The suture between the palatines and the ectopterygoid is not easily made out, but this region descends below the maxillaries to opposite the middle of the inside of the mandible, as in many *Lacertilia*. Just anterior to the oblique angle which marks this descent a ridge of the palatines extends forwards and outwards, and for a short distance bears a row of teeth. These teeth, like those of the internal palatine series, are in a single row, differing in

this respect from the species of *Pariasaurus*, as described by Seeley, where they are in two rows period. The positions of the rows are the same in the two genera. The posterior border of the ectopterygoid supports a patch of teeth in several rows. They are much less developed in *Pariasaurus*.

"The pterygoids are slender and diverge from the interior part of the palatines outward, backward and upward, to the inner side of the quadrate. They bear no teeth. The sphenoid is deeply grooved on the middle line as in *Elginia*. Its lateral inferior keels project below the plane of the short basioccipital. There is no evidence that any of the rows of teeth of the upper jaw rise from the palatine bone; they appear to be maxillary in attachment.

"The specimen of *Pariotichus aguti*, on which the above observations are made, possesses, attached to the skull in nearly normal relations, seven vertebrae, a good deal of the scapular arch, and the right humerus. The fifth and sixth vertebrae have slender cervical ribs. The bodies of these, with that of the seventh, are the only ones whose inferior surfaces are exposed. I observe narrow faces for intercentra between them. Of the scapular arch the clavicle and a median element are preserved. The former has a narrow subvertical portion which rests on the anterior edge of the scapula, and a horizontal portion which is considerably expanded, contracting gradually to the middle line. The median element is T-shaped, with the median portion or stem rather slender. It is broken off posteriorly so that its apex cannot be described. It underruns the expanded clavicles, and may be, therefore, supposed to be a cartilage bone and a true sternum, and not an interclavicle. A superficial layer of the exposed part of this element is roughened by sculpture, and probably represents the interclavicle. The inferior layer of the expanded part of the clavicle is similarly sculptured. The humerus has greatly expanded extremities and a slender shaft of moderate length. The form is similar to that of *Pariasaurus*. There is an angulation of the distal extremity which represents the condyle. Entepicondylar foramen well developed; no ectepicondylar foramen."



An analytical table gives the characters of the various species (p. 445):

I. The long maxillary tooth below the anterior border of the orbit.

Head short, wide; orbits small, half interorbital width; length of skull about 25 mm. . . . . *P. brachyops.*

II. The long maxillary tooth nearer the nostril than the orbit.

a. Sculpture reticulate.

Interorbital and parietal sculpture reticulate; interorbital width 20 mm.; interior jaw teeth with round crowns. . . . . *P. incisivus.*

aa. Sculpture more or less in longitudinal ridges.

Interorbital sculpture in longitudinal ridges; interorbital width 9 mm., equal orbit; maxillary tusk abruptly longer. . . . . *P. ordinatus.*

Cranial sculpture in longitudinal ridges; orbit about equal interorbital width; skull equilateral, straight posteriorly; length 72 mm.; inner jaw teeth compressed. . . . . *P. isolomus.*

Cranial sculpture partly reticulate, especially medially; orbit about equal interorbital width; width of skull three-quarters length; outline emarginate posteriorly, length 80 mm. . . . . *P. aguti.*

Orbit oval; cranium 162 mm. long, and nearly as wide; posterior border emarginate; muzzle much contracted, entirely overhanging symphysis mandibuli. . . . . *P. hamatus.*

To these was added *P. aduncus* in a later article (6), characterized by the strong decurvature of the anterior end of the muzzle and the gradation in the size of the maxillary teeth instead of the single abruptly large one.

As the specimen here described has been identified as *P. incisivus*, it is necessary to give the generic and specific characters of *Ectocynodon incisivus*, under which name it was originally described. The generic description was given in 1878 (1) (p. 508): "Cranium short and wide, with large post-frontal bones and a large orbit. Cranial bones sculptured, but no lyra. Teeth rhizodont with elongate compressed crowns with anterior and posterior cutting edges. One of these

between the orbit and the nostril larger and longer than the others, and lying outside of the closed dentary bone. Mandibular symphysis not sutural, but ligamentous. Terminal mandibular tooth not small. Teeth not faceted, simple."

The species *incisivus* was described in 1886 (5) (p. 291): "The muzzle is quite prominent, a character somewhat exaggerated in the specimen by pressure. The nostrils are large, lateral in direction, and situated close to the end of the muzzle. The orbits are sub-round, of medium size, and look mainly upwards in the present condition of the specimen. One of the most important peculiarities of the species is the disproportionately large size of the first or anterior incisor or premaxillary tooth. The crown is conical and nearly straight, with an acute apex slightly posterior to the central point. Its section at the base is slightly angulate. The two other premaxillary teeth are much smaller, the third quite minute and with a sharp apex.

"There are three maxillary teeth separated by rather wide interspaces, anterior to the large tooth, which give character to the genus. The latter is abruptly large, but not equal in dimensions to the large first incisor. Posterior to it the maxillary teeth are closely placed, and with obtuse crowns. They commence very small, and increase in size posteriorly. At a point where the palatine or ectopterygoid, as the fact may be, joins the maxillary, the tooth-bearing surface is wide, and supports four rows of small, obtuse-crowned spaced teeth of equal size. This dental patch is triangular, with its long angles extending anteriorly and posteriorly. The latter angle terminates a little posterior to the middle of the orbit. The teeth have a small axial pulp cavity, and the dentine is perfectly simple.

"The head sculpture is well defined, and is reticulated in pattern."

*Additional Description of the Head.*—On one side, in the specimen here described, there are sixteen maxillary teeth visible; allowing for lost teeth, there were about nineteen in the series; this number is probably not constant for the species. The enlarged maxillary tooth, which is only slightly larger than the adjacent teeth, is the sixth from the anterior end, probably the seventh of the complete series. Posterior

to this tooth the teeth become smaller and more irregular in position; they are smooth and without anterior and posterior cutting edges. The teeth of the mandible and the premaxillary are as described by Cope, with the exception that in the posterior part of the mandibular series only are the teeth arranged in more than one row. The dentine of the enlarged internal incisor of the premaxillary shows some indication of a radial arrangement of the dentine.

The upper surface of the skull is so injured that it is impossible to make out the exact relations of the bones, but their

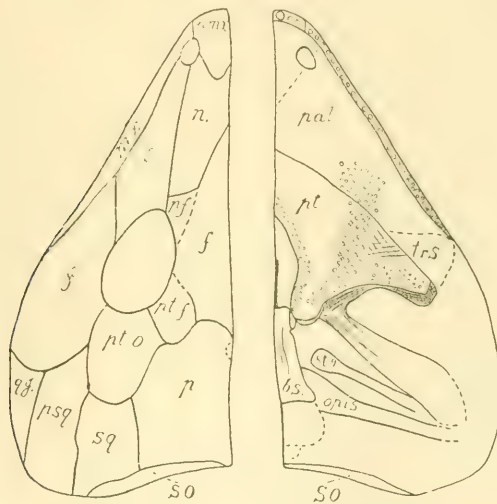


FIG. 1.—Upper and lower surfaces of skull. The extent of the lachrymal is adapted from Cope's figures, but is indicated in the present specimen as well.

general arrangement is shown in Fig. 1, in part suggested by Cope's figures. The character of the sculpture in the occipital and parietal regions is shown in Fig. 2.

The lower surface of the skull shows the general arrangement of the bones characteristic of the Permian reptiles; teeth are present in patches upon the vomer, palatines, and pterygoids. The pterygoids show the tripartite form characteristic of the *Pelycosauria*; the anterior process is broad and plate-like, and the anterior part of each bone joins that of the opposite side in the middle line; more posteriorly they diverge and form a vacuity, into which projects the stylus-like anterior end of the

basisphenoid (presphenoid): the edges of this vacuity are covered with small teeth set closely together. The posterior process is also broad and plate-like; it extends back to the quadrate which it joins; it is set at something of an angle with the rest of the bone. The third process is not so distinct from the rest of the bone as in the *Pelycosauria*; it is virtually a thickening of the posterior edge of the anterior process, but this is carried to a degree that demands description as a separate process. It extends directly outward from a point opposite the middle portion of the bone; the posterior edge is sharp and abrupt, while the anterior side slopes down gently to join the rest of the bone; this slope is covered with a patch of small blunt teeth, very closely set together; the patch is separated from the patch upon the borders of the median vacuity by a shallow groove; it is connected with the patch upon the palatine. The presence of this patch of many small blunt teeth upon the external process is one of the distinguishing features of the *Pariotichidae*, for in the *Pelycosauria* the teeth upon this process are few, and planted in distinct sockets. Opposite the origin of the external process there is developed on the inner edge of the bone a short blunt process, the basisphenoid process, which gives attachment to the basisphenoid bone (Fig. 1, *pt.*).

There is no trace of an ectopterygoid; it is probable that it was attached to the anterior process of the pterygoid, and did not join the external process except at the anterior side of the extreme end.

The basisphenoid is much as in other primitive reptiles, with the characteristic groove on the lower surface, between the basiptyergoid processes; the anterior end is continued as a long and slender process (presphenoid), which extends into the median vacuity between the pterygoids.

The posterior portion of the base of the skull is obscured by the crushed anterior cervical vertebrae and the distortion accompanying fossilization. A distinct opisthotic can be made out, and anterior to this a long slender element that appears to be a stapes. The basioccipital is completely obscured. The quadrate is covered by the bones of the temporal region and the articular portion of the lower jaw, but enough can be made out

to show that it was small and flat, and even in the natural condition was covered by the surrounding bones to a large extent. The arrangement of the bones of the lower surface is partly indicated in Fig. 1.

The lower jaw is of the same type as the modern *Sphenodon*; there is a rather low coronoid process, and the angle of the jaw extends posterior to the articulation.

*The Vertebrae.*—There are eighteen presacral vertebrae in the specimen; a break between the skull and the anterior end

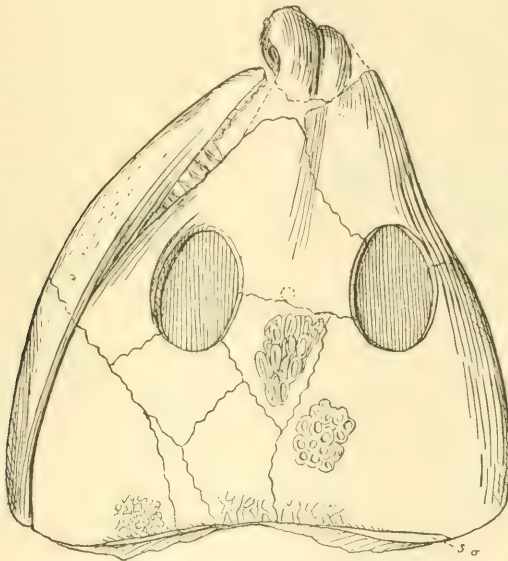


FIG. 2. — Superior view of skull. The sculpture of the surface is indicated in the different regions. *s.o.*, supraoccipital.

of the body suggests the possibility of one or more having been lost, but this is hardly probable; the author collected the specimen here described, and from the position of the bones and the condition of the matrix it seems that the column must be perfect. The number of presacrals is very interesting, as it is the characteristic number for *Pareiasaurus* and the turtles. The anterior two vertebrae have been badly crushed and lie upon the lower surface of the skull; enough can be seen to show that the atlas was a simple ring; the face for the occipital condyle shows that there was a better development of the



condyle upon the sides than in the middle, indicating a rather bipartite condition, such as is found to a greater degree in the *Gomphodontia*.

The vertebrae are all deeply biconcave, and there are wide spaces between the lower edges of adjacent vertebrae, which indicate the presence of intercentra. Between the seventh and eighth vertebrae there is a small bone which appears to be an intercentrum. The most striking thing about the vertebrae is their similarity to the vertebrae of *Parviasaurus*. The neural arches are broad and flat, with rather swollen sides and very prominent anterior and posterior zygapophyses, whose faces look straight up and down. The spinous processes are short

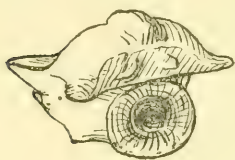


FIG. 3. — A posterior dorsal vertebra (natural size).

and stout, and seem to have been attached to some dermal ossification; in the anterior part of the column the processes are bifurcate. Fig. 3 will show the general appearance of a vertebra from the posterior part of the series. The most anterior of the connected series of vertebrae lies

immediately above the anterior ends of the coracoids; it has stout transverse processes that stand out at a right angle from the anterior part of the centrum and underlie for the most part the anterior zygapophyses; they are about as long as one-half the centrum. Attached to the transverse process is a long rib, wide at the two extremities and narrowed into a rather angular shaft in the middle portion; the proximal end is attached by the upper part to the transverse process, and by the lower to the intercentrum (the tubercula and capitula are not distinct). The distal extremity of the rib is wide and spatuliform; the whole rib is bent upon itself so that the two ends are directed at right angles to each other. The second vertebra bears a pair of ribs that differ from the first pair in that they are straight and longer; they are expanded proximally and distally. The transverse processes of the vertebrae grow smaller, until the last can be detected as a small tuberosity upon the ninth from the first rib-bearing one; it is probable from the size and rate of diminution that the last trace disappeared upon the eleventh; this would leave five verte-

brae without ribs. Other than the disappearance of the transverse processes and a gradual gain in stoutness, there is little change in the whole series (Fig. 4).

There are two vertebrae in the sacrum: the first bears a strong rib with an expanded distal extremity as wide as the length of the vertebrae; the second has a less well developed pair of ribs with the distal extremity hardly broader than the rest of the process (Fig. 5).

There are two caudal vertebrae attached to the sacrals; they are much the same in appearance as the others, and have short

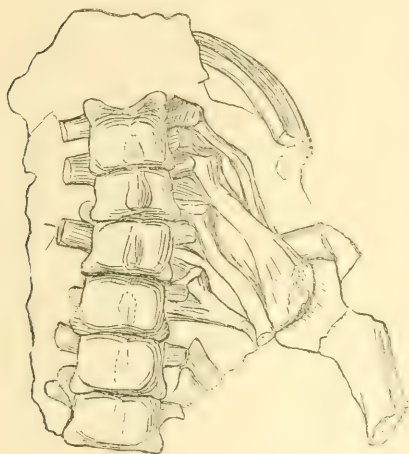


FIG. 4.—Dorsal view of anterior dorsal series.

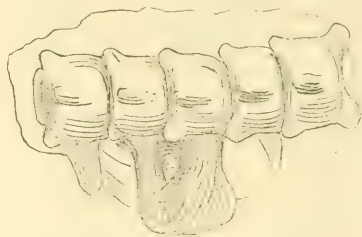


FIG. 5.—Dorsal view sacral vertebrae. The surfaces of vertebrae are restored.

strong ribs attached. A small fragment contains three caudals near the end of the tail; they show that the dorsal spines were much longer than in the dorsal region, and that there were rather long and slender ribs ankylosed to the vertebrae. Their size seems to indicate that the animal had a rather long tail.

The clavicles and the interclavicle are large and well developed, having much the appearance of the same bones figured by Cope in *Pariotichus aguti* (4) (Pl. VII, Fig. 2). The clavicle is there designated the episternum. The anterior end of the interclavicle is diamond-shaped in outline; the lateral parts of the head underlie the ventral ends of the clavicles; they have a rugose sculpture of fine lines. The posterior portion is continued into a cylindrical process at least twice as long as the rest of the bone; its distal end is somewhat rugose.

The clavicles are peculiar bones with spatuliform enlargements at either end; the ventral ends lie flat upon the interclavicle and coracoid; the dorsal end lies at an angle of about forty-five degrees to the ventral; the shaft is much smaller and has a triangular section; it is so bent that the two ends of the

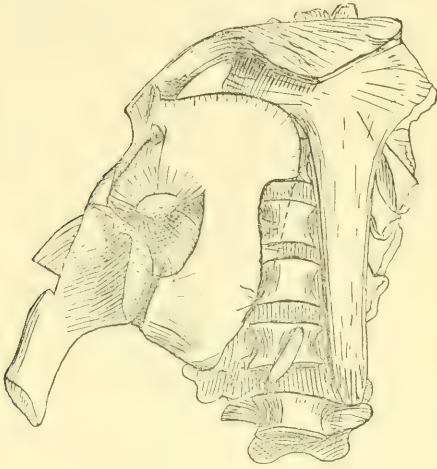


FIG. 6. — Ventral view of anterior dorsal series, showing pectoral girdle and humerus.

bone are directed at about a right angle to each other. There is no trace of any cleithrum (Fig. 6).

The scapula and the coracoid are united into a single bone, and there is no trace of any suture between them; the cotylus for the humerus is deep, and the rim is prominent above and below. The edges are complete, with no traces of any fossae or serrations. There is no trace

of any coracoid foramen. The outline of the bone is very characteristic, as there is a complete absence of the posterior prolongation of the scapula; it is much more like the form found in the amphibians of the same period (Fig. 6).

The lower surfaces of the vertebrae in the sacral region are covered by the remnants of the pelvis. The anterior ends of the ilia are broken away, but a separate fragment shows that it was rounded rather than acuminate; the distal end joined the proximal part by a rather slender neck. The ischium and the pubis were joined on the middle line and extended far anterior and posterior to the acetabulum. The acetabulum is rather large, and was imperforate. All three bones take part in its formation.

The humeri of both sides are preserved in an imperfect condition; the proximal end is expanded into a thin flat plate with a scarcely distinct head; the shaft is comparatively stout, and is triangular in section; the distal end is turned at almost a

right angle to the proximal portion. It is large and expanded, with no trace of an entepicondylar foramen. The absence of the foramen is rather a surprising feature, but is distinctly an amphibian character, it is present in *Pareiasaurus*; instead of the entepicondylar foramen there is a deep notch, such as represents the ectepicondylar foramen in the *Pelycosauria*. The ent- and ectepicondylar tuberosities are large and prominent, but the condyles are not well developed.

The radius and ulna are represented by the proximal ends only. The ulna shows a definite but not well developed olecranon fossa. The front foot of the left side has been preserved; the distal ends of the radius and ulna are nearly in their normal positions; the bones of the carpus are all present, with the possible exception of the first carpal of the distal row. There are well-formed scaphoid and cuneiform bones, and between these an elongate element that was at first regarded as the missing metacarpal I, but it seems more probable that it is the lunare (intermedium); the upper end is incomplete, and the lower is much the same in appearance as the end of the metacarpals; on the other hand, it occupies just the position of the intermedium, in a carpus that has been preserved in a very perfect manner, and it fits the position it occupies very accurately. According to this interpretation there are two centrale. There are four bones in the distal row of the carpus; the first is very much larger than the others, and appears to represent the first and second combined; the outer edge is a rounded process, with no face for articulation with another carpal. It is possible that the first metacarpal was attached to this bone with the second, but no traces of such a metacarpal remain. The metacarpals are short and stout, with well-developed articular condyles. The phalanges are not in contact with metacarpals, but a series which corresponds very closely to the fourth in size shows that they were also very short and strong. It is impossible to say whether there were more than three phalanges or not. Fig. 7 shows the arrangement of the bones very little altered from their position in the matrix.

The posterior limb is represented by the ends of the femur and of the tibia and fibula. The femur shows well-developed



articular surfaces. The tibia shows on the anterior end the deep groove which defines the cnemial crest.

The tarsus of the left foot is preserved, but the bones are somewhat displaced. There are eight bones. The most interesting thing about the foot is the fact that the proximal row is composed of two greatly enlarged bones that can only be astragalus and calcaneum; the astragalus is the larger, with strong articular faces for the calcaneum, and for the first and second tarsals of the distal row. The calcaneum is a large, round, and very thin bone that is preserved in the natural position; it articulates with tibia in common with the astragalus. The other bones of the tarsus are out of position, but one triangular-shaped bone lies over the astragalus and calcaneum; this seems to be the intermedium or, more likely, the centrale (naviculare); the intermedium having joined the tibiale to form the astragalus.



FIG. 7.

The five remaining bones are considered as belonging to the distal row, and the largest has been placed as the fifth, the fourth and fifth not having yet united to form the cuboid.

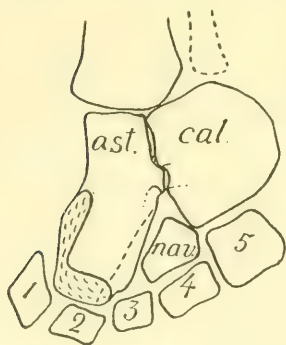


FIG. 8.

There is a separate fragment of bone that is so poorly preserved that it is impossible to say whether it is a complete bone or not; if it is it may be either a second centrale or the intermedium (Fig. 8).

The discovery of the well-differentiated astragalus and calcaneum throws a new light on the position of the *Cotylosauria*, for the proximal row of the tarsus in *Pareiasaurus*, as figured by Seeley, consists of a single bone; this difference must be considered as evidence in favor of the independence of Cope's order *Cotylosauria* from the *Pareiasauria*.



It will be seen that in many places the form here described departs from Cope's description of the type *Pariotichus incisivus*, but it seems best to assign it to the form which the previous fragmentary description most nearly indicates, and avoid the introduction of a new name until it may become necessary.

## Measurements :

Greatest length interclavicle . . . . .	77 mm.
Greatest breadth head of interclavicle . . . . .	23.5
Antero-posterior length of scapula coracoid . . . . .	52.5
Breadth of same at humeral cotylus . . . . .	36
Length of head on median line from back to point opposite middle of nares . . . . .	120.5
Interorbital width . . . . .	26
Breadth of skull at posterior end . . . . .	127
Breadth across orbits . . . . .	80
Breadth across nares (approximate) . . . . .	30
Length lower jaw . . . . .	150
Greatest length humerus . . . . .	66
Breadth lower end humerus . . . . .	30
Breadth lower end femur . . . . .	26.5

STATE NORMAL SCHOOL, MILWAUKEE, WIS.

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## ON THE PITHECOID TYPE OF EAR IN MAN.

HOWARD AYERS.

THERE have been relatively few contributions to our knowledge of the development of the external ear in man which give enough attention to such details as would render them useful to the anthropologist. For this and other reasons the following observations on the condition of the external ears in a three-months full-blooded negro foetus will doubtless be of interest, since they show in such an unmistakable manner the occurrence of a pithecoid ear in the human embryo, and thus give additional force to the conclusion derived from a study of comparative anatomy that the human races have descended from a Simian condition of structure. As Professor G. Schwalbe has already pointed out,<sup>1</sup> there are two methods which we may use in arriving at a knowledge of the past history of the human external ear. The first one, the method of comparative anatomy, has been most successfully employed, largely on account of the greater abundance of material for study; while the second method, that of embryology, has as yet yielded fewer results. Sometimes one, sometimes the other method gives us the best information regarding special facts, and it is only by the use of the knowledge gained from both sources that we may hope to reconstruct the phylogensis of the human ear.

Schwalbe has carried out the analysis of the mammalian ear from the comparative anatomical standpoint in a masterly way, and has shown that the Darwinian point, far from being of rare occurrence in civilized man, is present in three-fourths of all male ears and in nearly three-fourths of all male individuals, whereas it is present in less than one-half the total number of female individuals and in only about one-third of the whole number of female ears examined.

<sup>1</sup> Schwalbe, G., "Beiträge zur Anthropologie des Ohres," *Internat. Beiträge zur wiss. Medicin.* Bd., i. 1891.

The presence of this pithecoïd as distinguished from human character is thus the rule and not the exception among human males, reversing in this respect the general law of development among animals, that the female remains in a more primitive state of development than the male.

The ratio of the reduction of the ear in man beyond what we find in the lower apes is that of five to four in favor of the female.

It is interesting to note that while Schwalbe found the left ear to be, in general, more reduced, both in men and women, in the case which is here presented, it is the left ear which shows the *Cercopithecus* form, while the right ear approaches more nearly the normal human type.

This case is especially interesting on account of the additional information it gives of the details of the process of reduction of the auricular apex.

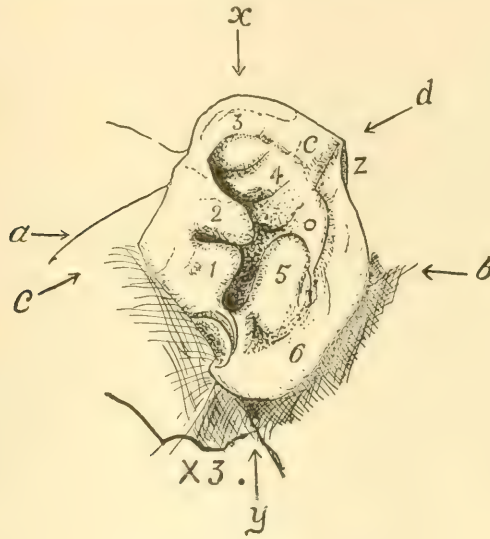
The apex of the ear lies upon the unrolled posterior border of the ear, above the anthelical line. It lies at the outer end of and forms the projecting spout of a trough which leads from the posterior (external) edge of the helical border forwards, downwards, and inwards, across the anthelical depression into the depths of the fossa angularis. This groove I have never seen in an adult ear, and only the faintest indications in other embryonic ears which have come under my observation.

Opposite the groove the mesal face of the lobe is carried out into a ridge which extends from Darwin's point towards the base of the ear, but does not reach it, fading out into the general level of this surface of the pinna.

The apical part of this ridge is shown in the figure at *s*, and can be seen here because of the slight out-flexure of the free border of the helix just below the Darwinian point. The border immediately above the apex shows no trace of flexure out of the plane of the pinna. The figure is carefully drawn to scale, enlarged three diameters. The shading, however, does not do justice to the original. The axes indicated by the arrows are the only ones I have thought worth while measuring, but any other measurements are readily had from the figure.

The axis  $x-y$ , or the physiognomic axis, measures 13 mm. The true long axis of the ear  $c-d$  is 10 mm. in length, while the greatest breadth along the axis  $a-b$  is 9.75 mm.

The lobe of the ear is sharply marked off from the general contour at its insertion into the side of the head by an indentation which is shaded too heavily in the figure.



EXPLANATION OF THE FIGURE.

1. Tragus.
2. } the modified embryonic tubercles forming the helix.
3. }
4. Anthelix.
5. Antitragus.
6. Taenia lobularis.
- z. Posterior fold of the pinna, its apex forming Darwin's point.
- $a-b$ . The true long axis of the ear.
- $c-d$ . Axis of the greatest breadth.
- $x-y$ . Vertical or physiognomic axis.
- Enclosed between 1, 2, and 5, the fossa angularis.
- Extending across from 2 to o, the crus helicus.
- Extending across from 2 to 5, the crus supra-tragicus.
- The arrow  $x$  points to the Saturnian point.
- Connecting 2 and o, the crus helicus.
- Connecting 2 and 5, the crus supra-tragicum, only traces of which are as yet present.

The two ears of the embryo are not alike in that the left ear displays the reversionary character to a much greater extent than the right.

The figure represents the left ear enlarged three diameters,



and it will be noticed that of the primary auricular tubercles 1, 2, 4, and 5 are especially prominent, as is usually the case at this stage of growth. But tubercle 4 is somewhat more prominent than ordinary. This is apparently not accidental, but is part of the general enlargement along the axis  $c-d$ , the original or ancestral long axis of the ear. Being in the third month of development, this ear presents us with the initial steps of the growth of the long axis of the ear, and of course it is during this period of development that we should expect to find ancestral traits best defined.

A series of observations which I have been able to make on the ears of very young children, for the purpose of locating and noting the degree of reduction of the Darwinian point, enabled me to study another character frequently associated with the Darwinian point which I believe has hitherto escaped notice. It is the presence of a tuft of relatively long hairs upon the Darwinian point.

This hair tuft seems to disappear later, as I have not observed it on any adult ear, though no extended series of adult ears has been sufficiently closely observed by me to satisfactorily settle the point.

Owing to the anthropological significance of this pencil or tuft of hairs, I propose for it the name Darwinian tuft. It is undoubtedly a remnant of the apical hair tuft commonly developed in the mammalia which often reaches special size as in the lynx.

UNIVERSITY OF MISSOURI,  
April 10, 1899.

# ZOÖLOGICAL BULLETIN.

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## CONTRIBUTIONS ON THE MORPHOLOGY OF THE ACTINOZOA.

### V. THE MESENTERIAL FILAMENTS IN *ZOANTHUS SOCIATUS* (ELLIS).

J. PLAYFAIR McMURRICH.

SEVERAL years ago I began a study of the mesenterial filaments of *Zoanthus sociatus* (Ellis), taking this form as a representative of the order Zoantheae, and intending, eventually, to extend my observations to other species and other groups. Various matters have, in the mean time, presented more pressing claims for attention, and I have so far been unable to carry out my original plan. I have, however, been able to study with considerable thoroughness the filaments of the adult *Z. sociatus*, and have also secured some data as to their development in bud embryos. I have not been successful in obtaining egg embryos of this species, but have observed certain interesting peculiarities in the development of the filaments in some zoanthid larvae whose parentage could not be determined; some of these I collected myself, while others I owe to the kindness of Mr. Alexander Agassiz, who obtained them by the surface net in West Indian waters.

It has seemed to me advisable, notwithstanding the imperfections of my material, to place my observations on record; the more so that it seems improbable that I shall be able to carry out my original plan of a thorough study of the filaments of the Anthozoa both from the histological and the embryological side.

## I. HISTORICAL.

Before considering the literature which refers especially to the filaments of the Zoanthidae, a brief review of the literature of the hexactinian filaments seems advisable, since it is in this group that the filaments have been most thoroughly studied.

Of the structures usually grouped together as parts of a mesenterial filament, the acontia, which are extruded from the body by the Sagartiadae, were naturally the first observed, having been described by Dicquemare in 1775, and, according to Con-tarini, by Gesner as far back as 1558. The first description of the filament proper of which I am aware was by Spix ('09),<sup>1</sup> but from his time onward frequent references to them occur. The older authors knew only that portion of the filament which we now term the *glandular streak* (Nesseldrüsenstreif), and they regarded this as a coiled tube occupying the free edge of the mesentery. The supposed tubular character of this structure led it to be considered either as a reproductive organ or a reproductive duct, a view to which Teale ('37) was the first to take exception. He, believing with Rapp ('29) that testes did not occur in the Actiniae, and that the ova developed without fertilization, and were rather "germ granules" or "gemmiferous bodies" than true ova, and recognizing that the filaments were not oviducts, suggested that they might be analogous to the salivary, pancreatic, and hepatic follicles of higher animals. Erdl ('42), by the discovery of testes, disproved the opinions of Teale and Rapp with regard to the organs of reproduction, but he, too, suggested a possibly hepatic function for the filaments.

The underlying idea of these suggestions of Teale and Erdl that the filaments were concerned in the digestive processes gained in popularity as new observations were added, while at the same time their direct homology with liver, pancreas, or salivary glands became more improbable. Without reviewing the various theories as to their function at greater length, it may

<sup>1</sup> I have not been able to consult the paper of Spix and know it only by a quotation given by Teale ('37).

be stated that their participation in the digestive processes seems to be now generally accepted, chiefly owing to the observations of Krukenberg ('80), and Metschnikoff ('80), and, more recently, of Willem ('93).

The earliest recognition of a difference in the structure of the upper and lower portions of the filaments was by Hollard ('51), who, however, merely noted its existence. A more careful description of the upper part of the filament was given by Haime ('54), who not only recognized the acontia and the glandular streaks, but speaks of the upper part as "gros cordons," each of which has attached to its sides "un feston très régulier et muni de cils puissants." Thorell ('58) also recognized the same three portions, terming the acontia "capsule cords," the glandular streaks "mesenterial threads," and the ciliated bands, on account of their proximity to the reproductive organs, "ovary cords."

Rathke, in 1840, had observed that the acontia of *Metridium dianthus* (*Act. plumosa*) were solid structures and not hollow, as had usually been supposed; and, a year later, Leuckart ('41) advanced the idea that the mesenterial filaments were also solid. Some later authors, such as Haime and Thorell, adhered to the earlier ideas; but Gosse ('60) described them as cords and named them craspeda, failing, however, to recognize the ciliated bands.

The first careful study of the filaments by modern methods was made by von Heider ('77). He confirmed Leuckart's observations as to their solidity, showing that the central axis of the filament was really the expanded edge of the connective tissue (mesogloea) of the mesentery. He also figured the trilobed condition of the upper part of the filament, but failed to perceive the peculiar nature of the epithelium of the lateral lobes, each of which according to his idea "das für die Mesenterial-filamente charakteristische Epithel trug." He seems, indeed, to have regarded the lobes merely as coils of the glandular portions of the filaments.

Finally, in 1879, the brothers Hertwig gave a very thorough account of the structure of the hexactinian filaments, and practically nothing has been since added to our knowledge of them.

The Hertwigs showed that they are solid structures and that two portions are recognizable (three in the Sagartiadae which possess acontia). The upper portion consists of two wing-like lamellae attached to the edge of the mesentery, which, in consequence, presented a somewhat trilobed condition in transverse section. The two lateral lobes are characterized by the epithelium of their outer surfaces being composed of long and very narrow cells, each of which bears a single cilium. These cells vary somewhat in length at regular intervals, so that longitudinal sections show the lobes to have a wavy contour. No glandular or nematocyst cells occur in this portion of the filament, which the Hertwigs termed the *Flimmerstreif*.

The lower portion consists of a more or less coiled cylindrical cord attached throughout its entire length to the edge of the mesentery. Its epithelium consists of gland cells, nematoblasts, supporting cells (Stützzellen), and sensory cells, the nerve fibers from these last forming a plexus between the bases of the other cells. This portion was termed the *Nesseldrüsenstreif*. In its upper part it is an almost straight cord, and in perfect mesenteries is continuous with the central lobe of the ciliated bands, and through this with the stomatodaeal ectoderm; in imperfect mesenteries, however, there is no such continuity with the ectoderm, the glandular streaks gradually fading out above, and, the central lobe of the ciliated bands being wanting, the lateral lobes are separated by a depression lined by ordinary endoderm cells. It would seem from this that the central lobe of the ciliated bands is in reality the upper part of the glandular streak.

The arrangement just described may be regarded as the typical one for the hexactinian filaments, though certain departures from it have been observed. Thus in the Madreporaria the ciliated bands have not yet been observed, and they are also absent in certain Actiniaria, such as *Protanthea* and *Gonactinia* (Carlgren, '93) and *Corynactis*, *Ricordea* and *Rhodactis* (Duerden, '98).<sup>1</sup>

<sup>1</sup> I may state that I can confirm Duerden's observation as to the absence of the ciliated bands in the last two forms.

So far, however, as the majority of the Hexactiniae are concerned both parts occur.



In the Zoantheae the ciliated bands are, as a rule, the most striking portions of the filaments, and, consequently, have received more attention than the glandular streaks. The earliest writer on the filaments of the Zoantheae, Lesueur ('17), describes, however, both portions in *Zoanthus solanderi* and in *Palythoa (Corticifera) glauco*. He described white filaments bordering the edges of the mesenteries and noted that above, attached to the base of the stomach, there were "thick white arcuated organs, striated in annulations, folded on each other and divided through their whole length by a small canal." He thought that the ciliated bands, or, as he called them, the arcuated organs, might "be considered as performing the functions of the liver."

Dana ('46) described the glandular streaks in *P. caesia* as spermatic cords and noted that "above the spermatic cords there is attached to each larger lamella, immediately below the stomach, a pair of flat branchia-like organs." Verrill, who observed these same structures in 1869, agreed with Dana in regarding them as branchiae, and they were again briefly described by Andres in 1877. None of these authors, however, seemed to regard the "branchia-like" or "arcuated" organs as parts of the mesenterial filaments, nor did Andres nor Verrill perceive their identity with the ciliated bands of the Hexactiniae which had been described by Haime and Thorell. This was left for R. Hertwig ('82), who described them as portions of the mesenterial filaments of his *Z. danae* (?) and pointed out that it is quite erroneous to consider them as structures peculiar to the Zoantheae.

Erdmann ('85) described both the glandular streaks and the ciliated bands, adding, however, nothing to our knowledge of their structure; and Koch ('86) failed to find mesenterial filaments in the forms which he studied, and maintained that they were not present, at least in the same form as in other actinians. Three years later I described ('89) the two portions of the filaments of *Z. flos-marinus*, and, in addition, noted that the cells covering the surfaces of the mesenteries for some distance outwards from the glandular portions of the filaments were much higher than the general endoderm, and were loaded

with green granules and fragments of sponge spicules. I suggested that this region of the endoderm was essentially digestive in function, an opinion which has since been confirmed experimentally by Willem ('93) for the Hexactiniae.

Haddon and Shackleton ('91 and '91a) confirmed my observations on other zoanthids and pointed out that slight variations in the form of the ciliated lobes occurred in certain forms, such as *P. axinellae*. Finally, von Heider ('95), in his description of *Z. chierchiae*, entered somewhat fully into the structure of its mesenterial filaments. He found in the ciliated bands what he regarded as a distinct area intervening between the central lobe and the ciliated portions of the lateral wings, and characterized by possessing numerous gland cells. He terms it the glandular swelling and attributes to it a digestive function. He also observed the heightened epithelium lateral to the glandular portions of the filaments which had been described by Haddon and Shackleton, and myself, but objects to its interpretation as a digestive area, believing it to be the region in which the reproductive cells are to develop, none of the specimens which he examined possessing these cells.

## II. DESCRIPTIVE.

### 1. *The Ciliated Bands.*

To correctly interpret a series of transverse sections of an adult *Zoanthus* it is necessary to understand the course of the free edge of the mesentery. For this purpose I made a wax reconstruction of the upper part of one of the perfect mesenteries of *Z. sociatus*, together with the portion of the stomatodaeum to which the mesentery was attached. From this it is evident that the lower edge of the stomatodaeum is bent back upon itself, as represented in the diagram (Fig. 1), and that its ectoderm becomes continuous with the epithelium of the large ciliated bands. From the reflected stomatodaeum the free edge of the mesentery, with the filament, extends outwards and then arches downwards. Consequently, in transverse sections through the column the filament will be cut practically longitudinally

above (Fig. 1, *DD*), then somewhat obliquely, and below transversely (Fig. 1, *AA*).

I have represented in Figs. 2-4 sections through the ciliated bands at approximately the levels indicated in Fig. 1 by *AA*, *BB*, *CC*, and *DD*. In Fig. 2 two mesenteries are shown, and the section probably not having been perfectly transverse and the amount of contraction not having been quite the same in each mesentery, the filaments are cut at different levels, *2A* approximately at the level indicated by *AA* in Fig. 1, and *2B* at the level indicated by *BB*. In *2A* the filament is cut almost transversely. The free edge of the mesentery is occupied by

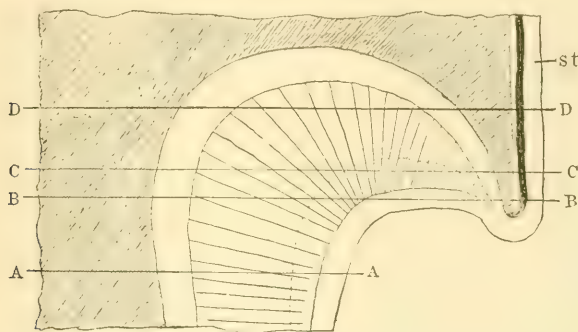


FIG. 1. — Diagram to show the relations of the ciliated bands. *st* = stomatodaeum; *AA* and *BB* = levels of sections shown in Fig. 2; *CC* = level of Fig. 3; *DD* = level of Fig. 4.

a tolerably high epithelium which contains numerous clear gland cells, probably mucous in character; the free edge of the mesogloea is somewhat expanded to support this epithelium, and, resting upon it, is a layer of very fine longitudinal muscle fibers. Probably a layer of nerve fibers is also present, but I could not be sure of it. From each side of the base of the expanded edge of the mesogloea a strong wing-like lamella arises, lined on the surface next the mesentery by endodermal cells similar to those of the surface of the mesentery; on the surface turned away from the mesentery, however, the epithelium is of a different nature. Nearest the free edge of the mesentery it consists of cells, for the most part resembling ordinary supporting cells (*Stützzellen*), with an occasional gland cell, containing numerous deeply staining granules, interposed. Towards the free edge of the lamella, however, the cells are very slender,

so that the nuclei seem closely packed, and are provided with rather long cilia; no gland cells are to be seen in this region. On one lamella of Fig. 2*A* these cells form a continuous layer occupying the greater part of the surface, at the attached edge appearing to dip under the less specialized epithelium. On the other lamella they are arranged in groups, separated by patches of less specialized epithelium, beneath which some of the groups,

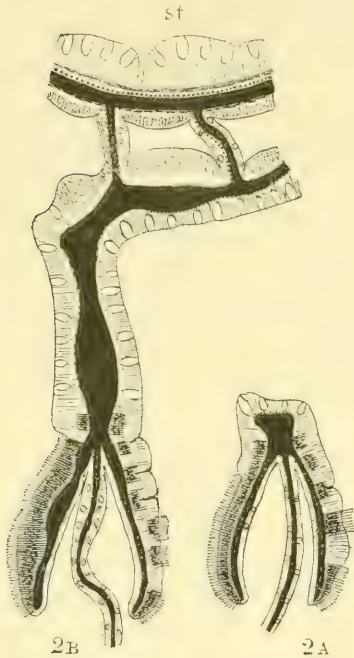


FIG. 2. *A* and *B*. — 2*A* is a section of the ciliated band at the level indicated in Fig. 1 by *AA*. 2*B* is at the level indicated in Fig. 1 by *BB*.

indeed, appear to lie. This latter arrangement is, however, merely an apparent one, and due partly to the contraction of the tissues and partly to the obliquity of the section of this lamella; all the groups are really at the surface in an expanded filament. The arrangement in groups, however, is a normal characteristic whose significance will be more readily understood from longitudinal sections, and the difference on the two sides of Fig. 2*A* is due to a slight difference in the plane on which the section passes through the two lamellae, one of which is probably slightly curved.

In 2*B* a section higher up, at the level indicated by *BB* in Fig. 1, is figured. It cuts the median portion of the filament longitudinally and shows clearly its histological continuity, and, it may be said, its histological identity with the stomatodaeal ectoderm. The structure of the epithelium of the lamella is the same as in 2*A*.

In Fig. 3 the section no longer cuts the median portion of the filament, but takes the wing twice nearly transversely and the intermediate portion, near the line of attachment of the wings to the edge of the mesentery, practically longitudinally. It is at the level indicated in Fig. 1 by *CC*, and the edge of the



region of attachment of the wings to the edge of the mesentery being indicated in this figure by the dotted line. In this section one sees the ciliated areas dividing the less specialized, or, as it may be termed, the *intermediate* epithelium, into a number of bands, a depression between each of these leading down to

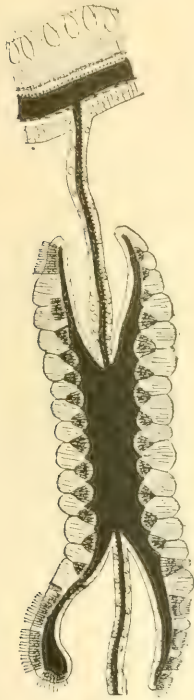


FIG. 3. — Section of the ciliated band at the level indicated in Fig. 1 by CC.

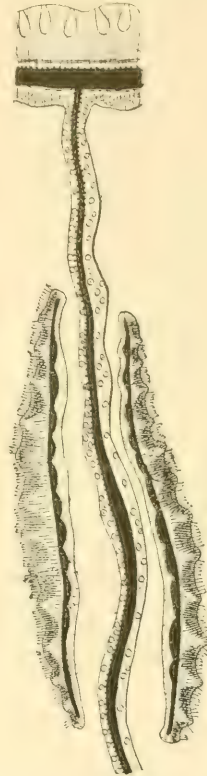


Fig. 4. — Section through the ciliated bands and a mesentery at the level indicated by DD in Fig. 1.

a group of ciliated cells, it being plainly evident that these latter do not reach the surface merely owing to the state of contraction of the tissues.

In Fig. 4 the section passes along the line indicated by DD in Fig. 1; that is, above the line of attachment of the lamellae to the mesentery. The intermediate portion of the ciliated band is again cut longitudinally and the marginal portion



obliquely. The arrangement of the ciliated cells in bands is clearly seen, the bands being much wider in comparison with the bands of intermediate tissue than in the last section, indications, indeed, of their continuity being shown by the short but narrow and closely packed cells which line the surface of each intervening ridge. Finally, it may be stated, in a section still higher up one finds a perfect continuity of the bands of ciliated cells, the section cutting the marginal ciliated cells longitudinally.

The general structure just described is essentially that described by previous authors, and more especially by von Heider ('95). My interpretation of the various parts differs, however, somewhat from that given by von Heider. He recognizes the intermediate epithelium, but regards it as an endodermal layer separating the marginal ciliated ectoderm from the median lobe of the filament, which he identifies with the glandular streak of the hexactinian filament. I shall return to a discussion of the nature of the epithelium of the median lobe later; in the mean time I may point out what seems to me a fundamental error in von Heider's interpretation. He regards the entire intermediate region of the wings as digestive in function, terming it the "Drüsenwulst," and identifying it with the endodermal areas of the glandular streaks which Willem ('93) has shown to be digestive.

As a matter of fact, there are two very different kinds of epithelium in this intermediate region; (1) that lining the furrows which run across it, and (2) that occupying the intervals between the furrows. The former is exactly like the epithelium found at the free margins of the lamellae, and is, indeed, continuous with this. In other words, the ciliated epithelium, which forms a continuous streak near the free edge of each lamella, sends inwards almost to the free edge of the mesentery a number of prolongations which line the bottom of depressions on the surface of the lamella. Each of these prolongations is separated from its neighbors by a non-ciliated band (at least, I have not been able to detect cilia in my preparations) of epithelium. It is this arrangement of the ciliated cells in transverse streaks which produces the characteristic transversely striated appear-

ance of the lamellae noted by nearly all observers, and it is interesting to note that Thorell in 1858, with his usual accuracy, described the arrangement of the ciliated cells in transverse streaks in the ciliated bands of *Metridium dianthus*.

The intermediate area cannot then be regarded as consisting wholly of endoderm, since it is generally admitted that the ciliated cells are ectodermal. Is then the intermediate epithelium endodermal and digestive? This is a question difficult to answer, but it may be said that the epithelium is certainly continuous with the stomatodaeal ectoderm above, and not with the endoderm. I do not find it essentially glandular in *Z. sociatus*; indeed, it contains relatively few gland cells in comparison with the epithelium of the median lobe. Those which do occur, however, are very different from the usual stomatodaeal glands with clear contents, since they stain deeply and are packed with granules. It is possible that such glands are digestive in function; they are especially abundant, as will be seen later, in the glandular streak of the filament, but they also occur here and there in the stomatodaeal ectoderm, and their occurrence in the intermediate epithelium cannot be accepted as evidence of its endodermal nature. From the evidence at my disposal, I am inclined to regard the intermediate epithelium as being ectodermal, as is the rest of the ciliated band epithelium, and think it erroneous to homologize it with the digestive, or rather ingestive, area described by Willem, which is unquestionably endodermal. I think, however, that intracellular digestion does occur in this epithelium, as I have seen imbedded in it particles which were neither zoöxanthellae nor normal constituents of the tissue, but which may have been ingested food particles.

## 2. The Glandular Streak.

Following a series of sections downwards below the level indicated in Fig. 2A, one finds the lamellae of the ciliated bands extending downwards for some distance, but they finally disappear, the median lobe of the filament alone persisting. The general appearance of the glandular streak has been

described and figured frequently, and reference may be made to the figures given by von Heider ('95), Haddon and Shackleton ('91), and myself ('89). The epithelium of this part of the filament forms a rounded or crescentic layer resting upon a somewhat *T*-shaped enlargement of the edge of the mesogloea. The tips of the crescent extend to about the tips of the transverse limb of the *T*, the outer surface of the limb being covered by a very different kind of epithelium, generally admitted to be endodermal. The general surface of the mesogloea of the mesentery immediately external to the attachment of the *T*-shaped enlargement is covered by a thick endodermal epithelium, which, traced outwards, gradually diminishes in thickness to pass into the ordinary epithelium of the mesentery.

In *Z. flos-marinus* I found ('89) in this thickened epithelium numerous foreign bodies, and suggested that it was a special region for intracellular digestion. Haddon and Shackleton ('91a) have described the thickening in *Z. macgillivrayi*, and von Heider in *Z. chierchiae*, — the latter, however, taking exception to my interpretation of its function, believing it to be the area in which the reproductive elements will develop. This idea is readily disproved by the examination of specimens in which the gonads are developed. For instance, I have preparations of *Z. nymphaeus* which show the thickened endoderm very distinctly crowded with foreign bodies, and, quite externally to this, in the region where the endoderm has assumed its usual low form, the sexual cells are found. On the other hand, my interpretation is confirmed by Willem ('95), for it is in exactly the region of the thickening that he finds an abundant ingestion of carmine particles in the Hexactiniae, these forms also presenting thickenings of the endoderm, usually less pronounced than in the zoanthids, immediately external to the glandular streaks of the mesenterial filaments.

It is very generally believed that the epithelium of the middle lobe of the ciliated bands is in direct continuity with the epithelium of the glandular streak; indeed, it has generally been regarded as the upper part of the glandular streak. It appeared that there was a marked difference in *Z. sociatus* between this median epithelium and that of the glandular

streak, and to test the accuracy of this appearance I endeavored to obtain a longitudinal section of the filament which would cut the epithelium of the median lobe above and the glandular streak below. After many trials I obtained a series, from three successive sections of which it was easy to reconstruct a median section through the filament. Such a reconstruction is represented in Fig. 5, somewhat diagrammatically.

In Fig. 6 is shown the appearance of a portion of the stomatodaeal ectoderm from the region indicated in Fig. 5 by *a*. It will be seen from this that the epithelium in this region is high, and that it contains numerous gland cells with clear contents; gland cells with granular contents are, on the contrary, rather rare. In addition, some darkly staining, slender, probably sensory cells occur, the rest of the tissue being composed of ciliated cells which stain only moderately, and are probably supportive cells. As I have already stated, the median epithelium of the ciliated bands is continuous with this above, and is histologically identical with it. Tracing the section downwards, however, it will be found that the median epithelium gradually becomes lower, and, at a certain region, it changes somewhat abruptly its histological character.

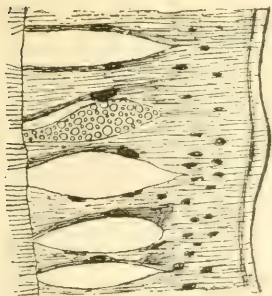


FIG. 6. — Portion of Fig. 5 about the region marked *a*, more highly magnified.

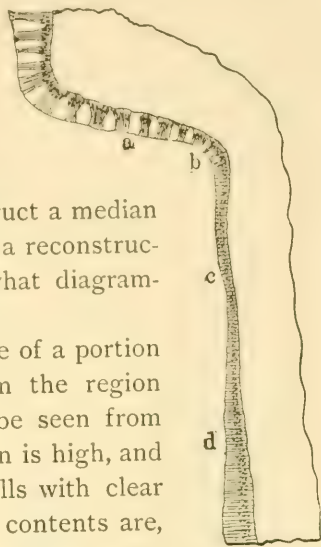


FIG. 5. — Reconstruction from three sections of a longitudinal section through the stomatodaeum, the median lobe of the ciliated band and a glandular streak of *Z. sociatus*. *a-d* = the levels from which Figs. 6-9 are taken.

Fig. 7 represents a portion of the epithelium at the region where the change takes place (*b* in Fig. 5). The upper part of the portion figured is essentially the same as the stomatodaeal ectoderm, but in its lower part there appear cells which stain somewhat darker than the ordinary supporting cells and have



large oval nuclei situated about the middle of their length. At the same time the large mucous gland cells disappear. Lower still (at *c* in Fig. 5) the change is complete and an entirely new form of epithelium occurs (Fig. 8). In this the cells are still lower; they contain large oval nuclei arranged in about two or three layers at the middle part of the epithelium, and there is apparently an entire absence of gland cells. I could not distinguish cilia in this region in my preparations, but am not prepared to say that they do not exist.

Following this stretch of tissue downwards, it is found to change again to form the epithelium of the glandular streak



Fig. 7. — Portion of Fig. 5, about the region *b*, more highly magnified.



Fig. 8. — Portion of Fig. 5, about the region marked *c*, more highly magnified.

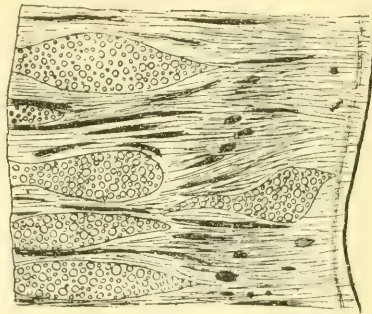


Fig. 9. — Portion of Fig. 5, about the region marked *d*, more highly magnified.

(Fig. 9). This is very high again, higher even than that of the stomatodaeum. It consists, like the latter, of supporting, sensory, and gland cells, but the gland cells are all of the kind with granular contents. I have found no nematocysts in the glandular streak of *Z. sociatus*, but their absence is by no means peculiar to that form.

It is clear then that in *Z. sociatus* there is neither a histological continuity nor a histological identity of the upper part of the median streak of the filament with the lower or glandular streak proper. The upper part is merely a continuation downwards of the stomatodaeal ectoderm, and this gives place to a low epithelium destitute of gland cells and of a generally indif-



ferent character, below which the characteristic epithelium of the glandular streak comes into view. It seems to me from these results that one is not justified in assuming, as has so frequently been done, that the glandular streak epithelium is a prolongation of the stomatodaeal ectoderm. What I have just described, taken in conjunction with the observations of E. B. Wilson ('84) on the development of the filaments in the Alcyonaria, and with what I have found ('91) as to their development in the Hexactiniae, seems to me rather to point to a complete distinction between the two kinds of epithelium, and I regard the structure of the adult filament of *Z. sociatus* as confirmatory of the conclusions obtained from embryological studies, that the ciliated bands of the filaments are ectodermal in origin, while the glandular streak proper is an endodermal structure.

### III. THE DEVELOPMENT OF THE FILAMENTS IN EGG EMBRYOS.

The material at my disposal for the study of the embryonic development of the filaments was not sufficient for an exhaustive study of the subject. The youngest larvae already possessed twelve mesenteries arranged in the manner described by van Beneden ('90) and myself ('91a). On none of the mesenteries were there any indications of the ciliated bands, but, on the other hand, the glandular streaks were plainly indicated on the perfect mesenteries as an epithelium occupying the free edge of the mesentery and composed of cells with closely set, elongated, and deeply staining nuclei, very different from those of the general endoderm of the mesenteries. But what is more interesting, on the lower part of the free edge of each of the imperfect mesenteries a similar, but smaller, patch of epithelium was plainly visible. In Fig. 10 is given a representation of a part of a section through the lower portion of the column of one of these youngest larvae. Owing to its base having been somewhat depressed by contraction, this has been cut towards the central part of the section. Transverse sections of four mesenteries are shown; the two larger mesenteries are one of the macrodirectives (III), and one of those which I have taken for

the first formed (I), and the two smaller are those indicated in a previous paper ('91a, Pl. IX, Fig. 6), as V and VI.

The larger mesenteries, when traced upwards, are seen to become attached to the stomatodaeum, while the smaller ones are imperfect. The epithelium which represents the glandular streak seems to be continuous above with the ectoderm of the stomatodaeum in the cases of the perfect mesenteries, though close examination shows some slight differences in the two epithelia. In the cases of the imperfect mesenteries such a continuity is out of the question, and there is not the slightest indication of a band of ectoderm extending up the outer wall

of the stomatodaeum, across the under surface of the disc and thence down the free edge of the mesentery, by which a connection between the glandular streak and the stomatodaeum might be accomplished. The glandular streak epithelium can be traced upwards upon the imperfect mesenteries to a level a little above the lower edge of the stomatodaeum, where it fades out, the free edges of the mesenteries being occupied from that point upwards

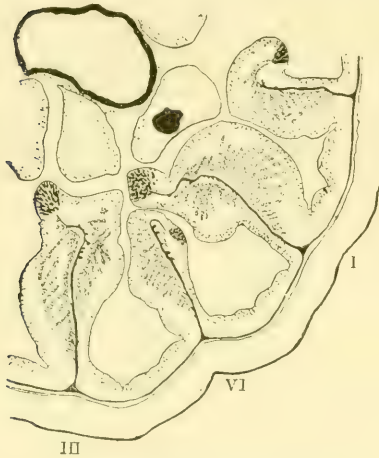


Fig. 10. — Transverse section through a portion of the column of a young zoanthid larva.

by cells of exactly the same nature as those covering their surfaces. That there may have been in an earlier stage some continuity between the stomatodaeal ectoderm and the glandular streaks of the imperfect mesenteries is possible; in my youngest embryos there are, however, no signs of any such connection.

In the adult condition mesenteries V and VI have no filaments (VI has in macrocnemic forms), and one might expect that older embryos would show a disappearance or diminution of the filaments of those mesenteries. In Fig. 11 is represented a part of a section through an older larva, in which the number of the mesenteries still remains at twelve. The filaments, how-

ever, have assumed an appearance much more like those of the adult, and the histological differentiation of their epithelium is quite pronounced. The mesenteries figured are the same as those shown in Fig. 10, but of the opposite side of the body. It will be seen that in mesentery VI all traces of the glandular streak have vanished, but in mesentery V the streak is still persistent, and indeed has undergone a progressive development, just as those of the perfect mesenteries. That this is not because the larva is the young of a macrocnemic species is

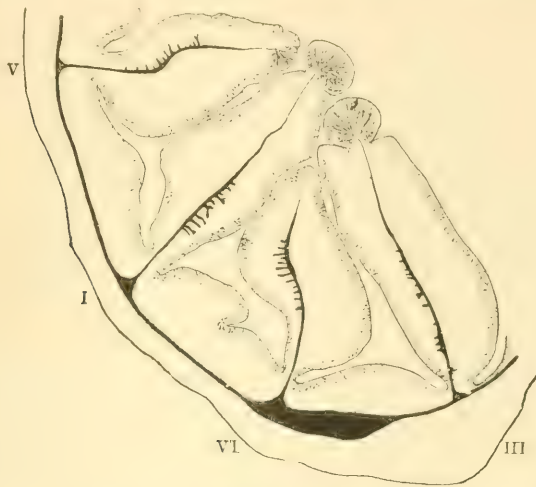


Fig. 11. — Transverse section through a portion of the column of a zoanthid embryo somewhat older than that from which Fig. 10 is taken.

shown by the fact that it is not mesentery VI, the additional perfect mesentery, in these species, which has retained its filament, but mesentery V. Probably later stages would show a disappearance of the filament of this mesentery also, but the point which is of concern is the fact of the development of filaments on these imperfect mesenteries whose epithelium is, so far as can be ascertained, at no point in contact with ectoderm.<sup>1</sup>

<sup>1</sup> Attention may be called to the fact that the discovery of filaments in these mesenteries serves to emphasize the correctness of the conclusion as to the order of the appearance of the mesenteries in the Zoantheae which has been stated by Boveri ('89) and myself ('91a), and I may add that indications of filaments in the microdirectives can also be distinguished, though they are much less evident than those of V and VI, possibly on account of an earlier degeneration.

#### IV. THE DEVELOPMENT OF THE FILAMENTS IN BUDS.

The time relations of the ciliated bands and glandular streaks in buds is just the reverse of what obtains in egg embryos; that is to say, the ciliated bands are the first to develop, the glandular streaks appearing later.

In a bud of *Z. sociatus* 2 mm. in length the stomatodaeum is already formed, and on the edges of the perfect mesenteries, immediately below the lower margin of the stomatodaeum, the ciliated bands can be seen presenting practically the same appearance as in adult polyps. Following a band downwards, it is found to disappear below and no trace of a glandular streak can be found, and no enlargement of the endoderm just external to the free edge of the mesentery. Indeed, there is nothing to distinguish a perfect mesentery from an imperfect one below the level of the stomatodaeum, except greater width. The free edges of both mesenteries is occupied by cells indistinguishable from ordinary endoderm except by their apparently somewhat smaller size.

The glandular streak begins to develop, however, soon after this stage, since in a bud but little older they were readily recognizable, and the ectoderm just external to them had become relatively high and was packed with foreign bodies; in buds 3.5 mm. in length all the parts of the filament occurring in the adult were present.

It is interesting to note that in the buds of *Alcyonaria* the same acceleration in the development of the ciliated bands has been observed by E. B. Wilson ('84), the glandular streaks in the egg embryos of these forms developing before the ciliated bands, as in zoanthids.

#### V. CONCLUSION.

I have shown above (1) that in adult polyps of *Z. sociatus* there is no histological continuity between the glandular streaks and the ciliated bands; (2) that in egg embryos the glandular streaks develop before the ciliated bands make their appear-



ance; (3) that in the same embryos the streaks make their appearance on mesenteries that are not connected in any way apparently with the ectoderm, and (4) that in bud embryos the ciliated bands appear before the glandular streaks.

It seems to me from these facts that the ciliated bands must be regarded as being ontogenetically distinct from the glandular streaks. The two have been very generally regarded as different parts of the same structure, but this idea is, I think, untenable.

If they be recognized as distinct structures, there are no *a priori* reasons for regarding both as products of the same germ layer. The question of the origin of the filaments, whether from the ectoderm or from the endoderm, is one that has been frequently discussed, and with very varying answers. The majority of authors have regarded both parts as ectodermal or as endodermal, E. B. Wilson having been the first, from his studies on the Alcyonaria, to point out the probability of the development of the ciliated bands in these forms from the ectoderm and that of the glandular streaks from the endoderm. In my studies on the development of the hexactinians ('91), I reached the same conclusion, and the evidence presented above seems to point to a similar story in the zoanthids.

However, there is a more fundamental consideration at the base of all questions as to ectodermal and endodermal origin in the Coelentera. Is there sufficient fixity of the germ layers in these forms, whether the layers be regarded from the morphological or the physiological standpoint, to warrant the importance which has generally been attached to them? The germ layers have evolved; like other structures, they have had a phylogeny, and it may be remarked that just as in other structures we find discrepancies between the phylogenetic and ontogenetic development, so too we may expect and undoubtedly do find discrepancies between the ontogeny and the phylogeny of the germ layers. It has generally been accepted that the Coelentera represent a stage in the phylogeny of the germ layers, two of them being fully differentiated; indeed, Huxley's homology of the coelenterate ectoderm and endoderm with the epiblast and hypoblast of the embryologists may be regarded



as one of the foundation stones of the germ-layer theory. But, after all, can we directly homologize the embryological and coelenterate layers? Are the coelenterate layers morphologically differentiated? It seems to me that they are not; every kind of cell, glandular, muscular, sensory, ganglionic, and even nematoblastic, which we find in the ectoderm, occurs also in the endoderm. The Coelentera represent a stage in the evolution of the diploblastic condition, rather than the completion of that condition, and we are assuming too much when we make a direct homology of their ectoderm and endoderm with the epiblast and hypoblast of, let us say, a vertebrate embryo.

I have spoken of only two layers in the Coelentera, omitting the mesogloea. This term, now generally accepted for the intermediate layer of the Coelentera, is sufficient reason for so doing, since it implies a lack of homology of the intermediate layer with the mesoderm of higher types. It seems to me, and I have so expressed myself elsewhere, that, if we are to seek for a homologue of the coelenterate mesogloea in higher forms, we must look for it in the limiting membrane which occurs just below the ectoderm. Indeed, a comparison of the mesogloea with the limiting membrane of certain polyclades is exceedingly instructive.

If, then, we regard the Coelentera as presenting merely an approximation to a diploblastic condition, the distinction between an ectodermal and an endodermal origin of any of their parts becomes relatively of little moment. And, furthermore, we need not be surprised to find that structures which in certain antimeres develop from one so-called germ layer, may arise from the other in other antimeres. This may be the case with the glandular streaks, and both those who have spoken in favor of their ectodermal origin and those who have maintained that they were endodermal may have right on their side. The observations of Goette ('93) and Miss Hyde ('94) have given reasons for believing that, in the Scyphomedusae, while the first pair of radial chambers is endodermal, the second pair is ectodermal in origin. If such variation occurs in this group in connection with such fundamental structures, surely we may meet with variations in the origin of the glandular

streaks in the Anthozoa. H. V. Wilson may be quite correct in maintaining an ectodermal origin for the glandular streaks of the first four mesenteries of *Manicina* ('88), and altogether wrong when he extends this origin to the streaks of the later formed mesenteries.

I would conclude, from my own observations, that the ciliated bands are probably in all cases ectodermal, and that, in some mesenteries at least, the glandular streaks are endodermal; yet I am prepared to accept as correct the ectodermal origin of the glandular streaks in other mesenteries. It is to be understood that I use the terms "ectodermal" and "endodermal" here merely for convenience and not as expressing a definite homology.

ANATOMICAL LABORATORY,  
UNIVERSITY OF MICHIGAN,  
March 13, 1899.

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## THE UNPAIRED ECTODERMAL STRUCTURES OF THE ANTENNATA.

MINNIE MARIE ENTEMAN.

A STUDY of the Strepsiptera, and an attempt to relate their peculiar reproductive system to that of other insects, first suggested the homologies which it is the object of this paper to establish. The material was furnished by Prof. W. M. Wheeler, of the University of Chicago, to whom I am also indebted for much kindly help and valuable suggestion.

The unpaired median ectodermal structures of insects are of two kinds: (1) chitinous apodemes, or fruceae, which occur in the thorax and serve for the attachment of muscles; (2) chitin-lined tubes or sacs, belonging to the various segments of the abdomen and forming the terminal, more or less differentiated portion of the genital ducts. A study of the occurrence of these structures throughout the Antennata, together with their embryonic development in a few forms, seems to indicate that they are homologous and derived from a series of segmental invaginations which were originally developed in relation to the appendages.

Considering first the apodemes: they are of very general occurrence throughout the insects, — we might even say the Arthropoda, — yet so far as I know little attention has been given to their structure and method of development. They usually consist of rod- or *T*-shaped inward projections from the intersegmental portion of the chitinous integument. Sometimes these projections are solid, but oftener they are hollow throughout their external third or fourth, thus giving evidence of their invaginate origin. The various parts may be bent or curved and give rise to minor projections, and their appearance may be further complicated by the union of successive apodemes. The free ends give attachment to muscles, and the intermediate part supports the connectives of the nerve chain.

The accompanying schematic figure after Graber will serve to give an idea of their usual form and function. *x* represents the apodeme in cross-section between two successive thoracic segments; *m*, points for the attachment of muscles; *s*, support for the nerve chain.

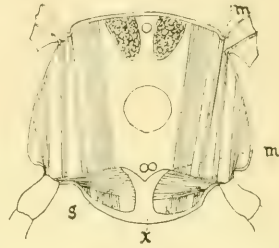


FIG. 1. — Transverse section through the thorax of an insect. (Schematic after Graber.) *x*, apodeme; *m*, points of attachment for muscles; *s*, support of nerve cord.

These structures reach their highest development and are most conspicuous where the power of flight is strongest, or locomotion is confined to only a few appendages. But we find a distinct beginning for them in the myriapods, where each body segment is provided with a pair of appendages. In *Scolopendra* (Fig. 3), for example, the intersegmental fold deepens toward the median line of the ventral body wall, and here we find attached two pairs of muscles. This intersegmental deepening is relatively uniform, with the exception of the first five segments of the body, where it is shallower to correspond with the slighter development of the legs.

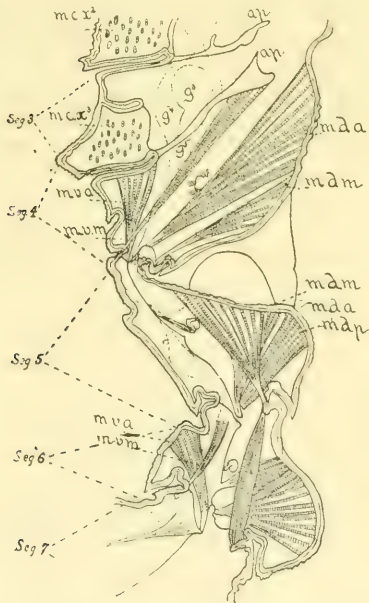


FIG. 2. — Sagittal section through *Myrmica rubra*. (After Janet.) *ap.*, apodemes; *g.* 3-5, ganglia; *m.c.x.* 2-3, muscles of coxae; *m.v.a.*, anterior ventro-lateral muscles; *m.v.m.*, longitudinal ventral muscle; *m.d.m.*, dorsal longitudinal muscle; *m.d.a.*, anterior dorso-lateral muscle; *m.d.p.*, posterior dorso-lateral muscle.

The accompanying figure of an ant, *Myrmica rubra*, shows the extent to which the development of the apodemes may be carried in a highly specialized insect. It represents a sagittal section through segments three to seven with the apodemes, to which the ventral longitudinal (*m.v.m.*) and the ventral lateral anterior muscles (*m.v.m.*) are attached. The dotted line represents the nerve cord.

Few observations have been made on the embryonic development of these structures. Ayers ('85), in his account of *Oecanthus niveus*, describes a median ingrowth between successive segments, which, as he states, atrophies late and "at the time of the closure of the dorsal wall of the body there is seen between the connecting cords of two adjacent pairs of ganglia a small triangular or cylindrical mass of cells, concerning the fate of which I am uncertain. I believe, however, they go to form a part of the internal skeleton. The chitinous rods in the thoracic region, to which the muscles of the legs and wings are attached, probably arise from the remnant of this median invagination, but in the abdominal region they may disappear entirely without giving rise to such structures."

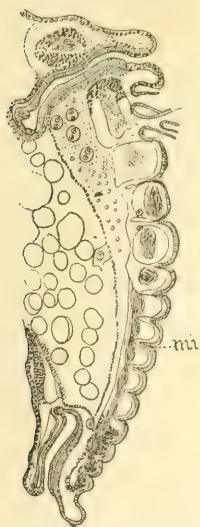


FIG. 4. — Median longitudinal section of embryo of *Oecanthus niveus*. (After Ayers.) *m.i.*, median invaginations.

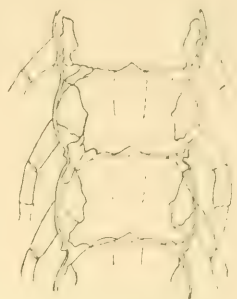


FIG. 3. — Two successive ventral segments of *Scolopendra*, seen from above, showing median deepening of the intersegmental depression.

Wheeler ('93) describes and figures a similar series of invaginations in the *Xiphidium* embryo extending through the thoracic and abdominal regions, of which he says the former "are converted into the chitinous apodemalous structures, which give attachment to some of the leg muscles." The latter disappear. This, of course, is just what we should expect if the abdominal ingrowth originally served the same purpose as the thoracic, but is now no longer functional. It is interesting to note, too, that in the embryos observed there occur evanescent traces of muscle-like cords running from the median ingrowth to the body wall (see figure).

Thus it appears that both comparative and embryological study indicate that the apodemes are parts of an originally metameric system of chitinous invaginations extending throughout the body and supporting the leg- and body-wall musculature.

Let us consider next the derivation of the terminal portion of the genital ducts. We rely here on some evidence of a more indirect character, but even then, it seems to me, the relations can hardly be questioned. In all the insect orders, with the exception of the male Ephemerids and some of the Dermaptera, the paired genital ducts open on the exterior through an unpaired terminal portion. This unpaired terminal portion arises independently from the integument, and during development comes into relation secondarily with the paired

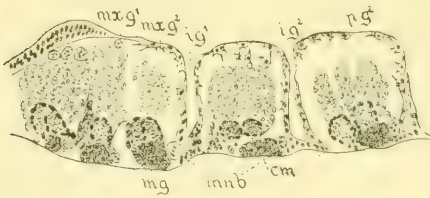


FIG. 5.—Sagittal section of the nerve cord of *Xiphidium ensiferum* a little to one side of median line. (After Wheeler.) *ig¹*, *ig²*, first and second interganglionic depressions; *mnb*, median cord neuroblasts; *mxg¹*, first maxillary ganglion; *mxg²*, second maxillary ganglion; *cm*, median cord. (?)

portion. It may be exceedingly slight in extent, as in the female Ephemerid, where it is merely a shallow depression between the seventh and eighth abdominal segments, the ovivalvula, as it is called, or it may be highly differentiated, as in the Dipteron, *Calliphora erythrocephala*,

where, according to Brüel, it includes in the male the seminal vesicles and the ductus ejaculatorius, and in the female the uterus, vagina, and vulva. Palmén ('84), in a series of sketches, has shown the varying limit between the parts of mesodermal and of ectodermal origin. These figures have been so extensively copied in text-books that I deem it hardly necessary to reproduce them here.

The position of the external genital openings is very various. In Chilopoda it is terminal in the last segment. In the female *Pauropus* it is near the posterior border of the second post-cephalic segment; the male apertures are paired, and the reproductive organs are otherwise so aberrant as to be hardly available for purposes of comparison. In most Hexapods the male aperture is between the ninth and tenth, the female between the eighth and ninth abdominal segments. In the Ephemeridea and some Orthoptera (*Blatta* and *Xiphidium*) the female opening lies behind the seventh segment. This instability in the position of the reproductive openings has been used



as evidence of origin from the homodynamous pairs of a series of metameric Nephridia and it seems to me that the argument might be similarly employed to account for the ectodermal portion of the sexual apparatus. Is it not probable that a primarily segmental Anlage made these conditions possible?

The condition of the Strepsiptera in this connection is most interesting. Here only the male undergoes complete metamorphosis. The female becomes sexually mature in the larval condition, and the young which develop from the egg in the body of the mother emerge through four median unpaired funnels, which open eventually near the posterior border of the second to the fifth abdominal segments, respectively. These funnels are curved toward the anterior part of the body and lined with chitin which is provided with outwardly directed spinules. Their general appearance reminds one strongly of the apodemes in some insects.

In the male there is a single genital aperture in the posterior border of the antepenultimate segment at the end of an unpaired chitin-lined ductus ejaculatorius. In both sexes the chitinous portions arise as unpaired ectodermal invaginations. The drawings give an idea of the conditions as figured by Nassanow ('92) for *Xenos Rossii*. My own study of the American *Xenos Peckii* gives identical results. Fig. 6 represents the three posterior segments of the adult male seen from above. *d.c.* is the ductus ejaculatorius; *v.d.*, the vas deferens; *t.*, testes; *m.*, muscles; *d.t.*, digestive tracts, with *c.*, coeca.

Fig. 7 is a sagittal section through a sexually mature female: *m.*, representing the mouth; *b.c.*, the brood canal; *b.f.*, brood funnels; *o.*, ova; *s.g.*, supra-oesophageal ganglion; *s.g.*, sub-oesophageal ganglion; *f.b.*, fat-body. Fig. 8 represents five stages in the development of a segmental brood funnel of the female, in which *e.* is used to designate ectoderm and *m.* mesoderm. Stage *D* persists during the development of the young, when the end of the funnel breaks through, giving place to Stage *E*.

The occurrence of funnels in four successive segments recalls the condition described by Heymons ('91) for *Blatta*, and Wheeler ('93) for *Xiphidium*, where the beginnings of the reproductive



system are segmental in the first to the sixth, and the second to the seventh segments, the metameric genital strand thus produced subsequently contracting and moving back to occupy



FIG. 7.



FIG. 6.



FIG. 8.

FIG. 6. — Three posterior segments of male *Xenos Rossii*, seen from above. (After Nassanow.) *d.e.*, ductus ejaculatorius; *v.d.*, vas deferens; *t.*, testes; *d.t.*, digestive tract; *c.*, coeca.

FIG. 7. — Sagittal section of female of *Xenos Rossii*. (After Nassanow.) *m.*, mouth; *b.c.*, brood canal; *b.f.*, brood funnels; *o.*, ova; *f.b.*, fat-body; *s.g.*, supra-oesophageal ganglion; *s.g.*, sub-oesophageal ganglion; *a.g.*, abdominal ganglion.

FIG. 8. — Five stages in the development of a segmental brood funnel. (After Nassanow.) *e.*, ectoderm; *m.*, mesoderm.

its usual position in the posterior part of the abdomen. The sexual organs are thus traceable to a primitive segmental type. Similarly the condition in *Xenos* may be regarded as the retention of a primitive character, as might be expected in a degen-

erate group such as the Strepsiptera. The primarily segmental Anlage, which made possible the varying conditions in the genital aperture, persists here in the development of ectodermal structures in four segments instead of only one.

The embryonic development throws further light on the origin of these structures. The conditions in *Xiphidium* and *Oecanthus* have already been described and figured. In the paper cited the abdominal invaginations are said to disappear, together with the rudiments of the abdominal appendages. And in a *Xiphidium* larva 3.5 mm. long the invaginations are seen for the most part to have grown much shallower, but the one lying just behind the ninth segment has grown only a little shallower and much broader, and has come to lie in close relation to the terminal ampullae of the genital ducts. This, then, is the pocket-like invagination, which later breaks through into the mesodermal ducts and becomes the ductus ejaculatorius. And we have here apparently the direct passing over of one of the segmental invaginations into the terminal ectodermal portion of the reproductive system.

We have, therefore, traced both the apodemes and the ectodermal part of the sexual ducts to a primitive condition, which is a mere median deepening of the intersegmental fold, arising in connection with the segmental appendages. This segmental arrangement of median ingrowths and appendages for all the body segments often occurs in the embryonic development of the higher Antennata, but the ingrowths for the most part disappear along with the ephemeral appendages. Only in the thorax, and here and there in the abdomen, they persist, become filled or lined with chitin, and, being brought into relation with the muscular or the reproductive system, serve as the apodemes or as the terminal ectodermal portions of the reproductive ducts in both sexes.

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HULL ZOÖLOGICAL LABORATORY,  
UNIVERSITY OF CHICAGO,  
May 17, 1899.

## SYNOPSIS OF THE CALLIPHORINAE OF THE UNITED STATES.

GARRY DE NORD HOUGH, M.D.

*Pollenia*. — Four species of *Pollenia* are recorded: *rudis* Fabr., *vespillo* Fabr., *glabricula* Big., and *obscura* Big. *Rudis* is very common and may be recognized by its brown abdomen, with white pollinose changeable spots. *P. varia* Meig. and *P. depressa* Meig. are small varieties of *rudis*. The description of *P. obscura* Big. applies exactly to many specimens of *rudis*. The abdomen of *vespillo* is shining black (Fig. 1).



FIG. 1.

*Chrysomyia* (*Compsonyia*). — *C. macellaria* Fabr. — Very common.

The metallic color of the body, the three black stripes on the thorax, and the yellow face make it easily recognizable. In this, as in all the Calliphorinae of metallic color, the shade

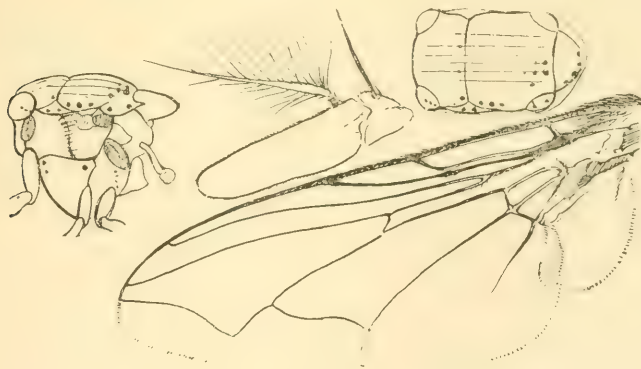


FIG. 2.

varies through violet, green, blue, and copper color, and since the color of the legs, antennae, and palpi also varies, it is not strange that its synonymy is too extensive for this article (Fig. 2).

*C. wheeleri* nov. sp., four males and two females (California). —From the collection of Prof. Wm. M. Wheeler, in whose honor I have named the species. Length 10 to 12 mm. Rather a blackish blue; more opaque than *macellaria*. As compared with its height, the head is broader than in *mac.*; height of bucca, 1.2 to 1.5 mm.; of eye, 1.8 to 2.0 mm. (average in *mac.*



FIG. 3.



bucca, 0.75; eye, 1.9). Front of male linear, of female one-third as wide as head. No orbital bristles; *mac.* has either two or one. Genovetical plates and vitta of female thickly beset with rather coarse, mostly black, hairs, among which

the usual transfrontal bristles can scarcely be made out. Palpi not filiform as in *mac.*, but club-shaped. Base of wing to apices of small basal cells blackish. Squamula thoracalis black, with white border; sq. alaris white, with black border. Thorax and scutel in both sexes thickly beset with long, soft black hairs,

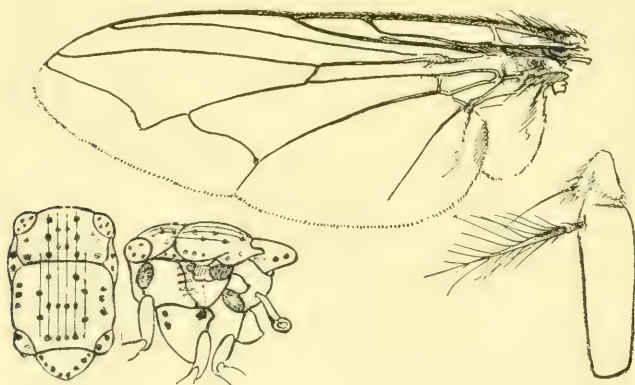


FIG. 4.

much longer than in male *mac.*; while female *mac.* has not hairs, but tiny bristles. Chaetotaxy as in *mac.*, but no visible posthumeral in any specimen, while *mac.* occasionally has a little one laterad the pre-sutural, or one further cephalad, or both (Fig. 3).

*Mesembrinella*.—Two Mexican, but no United States species recorded. Very likely will be found in our extreme south.



*Cynomyia*. — Our common species is probably *C. cadaverina* Desv. (Fig. 4). I described it as *C. americana* in *Ent. News*, May, 1898, and am indebted to Mr. Coquillett for pointing out the synonymy. *C. clongata* Hough (*loc. cit.*) may be distinguished by its more elongate form and the uniform presence of an anterior intra-alar bristle. *C. hirta* Hough, Alaska (*Ent. News*, September, 1898), has a golden yellow face and a long, dense coating of hair on thorax, abdomen, and legs.

All our *Cynomyiae* have a blackish blue, opaque, faintly striped thorax, a metallic green, blue, or violet abdomen, and black legs.

*Calliphora*. — All our species have reddish palpi, bluish black,

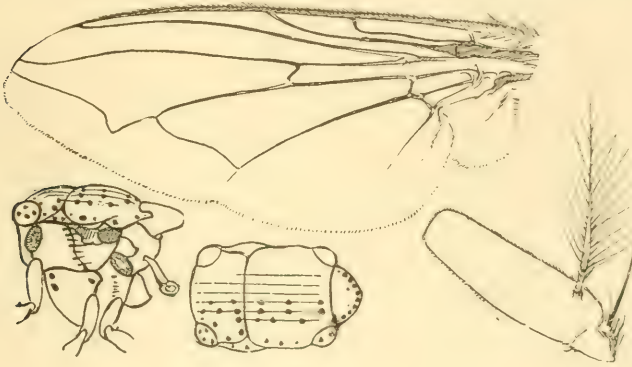


FIG 5.

opaque thorax, metallic blue or green, more or less whitish pollinose abdomen, and black legs. Chaetotaxy alike in all, except that a third posterior intra-alar bristle is regularly present in some species and regularly absent in others.

Bucca black, beard red; 3d post. i.a. rarely present . . . *vomitaria* L.

Bucca brownish or reddish, beard black; 3d post. i.a. rarely present  
*erythrocephala* Meig.

Bucca black, but with suggestions of red on its cephalic half, beard black;  
3d post. i.a. present; front of male one-fifth to one-sixth as wide as  
the head (in the preceding species not more than one-tenth)

*coloradensis* nov. sp.

Bucca black, beard black; 3d post. i.a. present; front of male not over one-  
tenth as wide as head, frequently linear . . . *viridescens* Desv.

Bucca black, beard black; 3d post. i.a. absent or minute; front of male at  
vertex (which is the narrowest part) one-fourth as wide as head; a  
second large pair of ocellar bristles present . . . *latifrons* nov. sp.

*C. viridescens* Desv. (1830), syn. *violacea* Meig. (1838), Fig. 5. — Prostigma usually black or dark brown. Abdomen in about half the specimens dull green, with pollinose coating instead of blue, as in *erythr.* Strobl has pointed out that this may be a



FIG. 6.

melanochroitic form of *erythr.*, but I think that the combination of the color differences with the uniform presence of a 3d post. i.a. proves the specific distinctness; only one out of several hundred specimens examined lacked the 3d post. i.a. Not very common; occurs especially in early spring and late fall.

*C. coloradensis* nov. sp., two males and four females (Colorado, C. F. Baker). — Prostigma black or dark brown. Abdomen dull green, with slight pollinose coating. Were it not for the male front being twice as wide, this might well be considered a connecting link between *erythr.* and *viridescens*.

*C. latifrons* nov. sp. (Fig. 6), eight males and twenty-eight females; Pullman and Seattle, Wash., C. V. Piper; Moscow and Craig's Mt., Idaho, J. M. Aldrich; Santa Barbara, Cal., Dyar; Mexico, O. W. Barrett. — Seven specimens have a minute 3d post. i.a. bristle. The second large pair of ocellar bristles (almost as large as the regularly situated pair) is about 0.05 to 0.1 mm. caudad, and about as much mesad the posterior ocelli. A stout costal spine just basad the end of the auxiliary vein; sometimes this is so appressed as to be seen with difficulty. Abdomen dull bluish green, with some pollinose coating.

I feel very certain of the following synonymy: *aurulans* Desv.,

*compressa* Desv., *mortisequa* Kirby, and *myoidea* Desv. are *Cynomyia* *cadaverina* Desv.; *obscoena* Eschholz is *vomitaria* L.; *lilaca* Walk., and *vicina* Desv. are *erythrocephala* Meig.; *terrae-novae* Macq. is *viridescens* Desv.

*Lucilia*.—All our species are of brilliant metallic colors. The chaetotaxy is invariable for each species, except for an occasional evident deformity, and it differs in the different species only in the number of achrostical bristles.

*Two postacrosticals* (Fig. 7).—Front of male linear, of female one-third as wide as the head; abdomen unicolorous . . . . . *caesar* L.  
Front of male not linear, at narrowest part about one-eighth as wide as the head; front of female about one-fourth as wide as the head; abdomen not unicolorous, first segment and hind margins of second and third blackish, contrasting strongly with the remainder

*pilatei* nov. sp.

*Three postacrosticals*.—Palpi black; front of male very narrow, that of female about one-third as wide as the head; abdomen with two stout marginal macrochaetae on the second abdominal segment

*sylvarum* Meig.

Palpi yellow; front of male varies from one-eighth to one-sixth as wide as the head, that of female about one-third as wide as the head; second abdominal segment without marginal macrochaetae (Fig. 8)

*sericata* Meig.

*L. pilatei* nov. sp., Tifton, Ga. Collected in June, August, September, and October by Mr. G. R. Pilate, in whose honor I

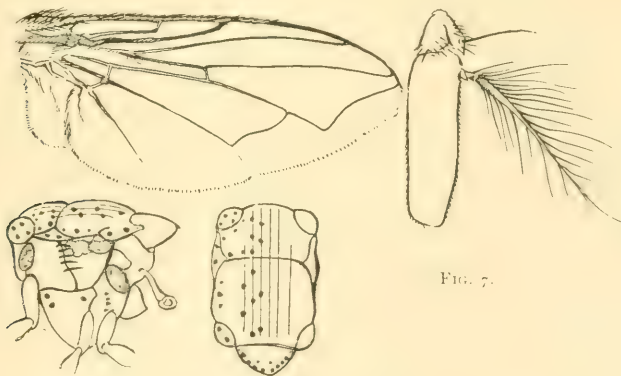


FIG. 7.

name it. Five males and seventeen females. Dorso ventral diameter of head greater, as compared with the transverse

diameter, than in *sericata*. Sides of ventral part of occiput and adjoining part of the bucca with a white beard. Anterior part of thorax by oblique light looks thickly white pollinose.

I have one specimen, male, New Bedford, which I refer to *L. caesar* L., because I can find no structural difference whose squamula thoracalis is blackish brown and whose halteres are

whitish at base of peduncle, the rest of the peduncle and the knob being blackish.

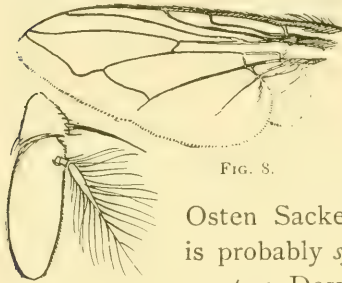


FIG. 8.

I offer the following suggestions as to the synonymy of some of the species of *Lucilia* recorded in

Osten Sacken's Catalog.: *L. brunnica* Desv. is probably *sylvarum* Meig.; *carolinensis* Desv., *compar* Desv., and *Heraca* Walk. are *Pseudopyrellia cornicina* Fabr.; *consobrina* Macq., *fraterna* Macq., and *lepida* Desv. are *caesar* L.; *caeruleiviridis* Macq. and *Sayi* Jaen. are *sericata* Meig.; *fulvifacies* Desv., *philadelphica* Desv., *terrae-novae* Macq., *mollis* Walk. (?), *rufipalpis* Jaen., and *stigmatalis* Thoms. are all *regina* Meig., as are also the following, described by Bigot in *Bull. Soc. Zool. Fr.*, 1887, — *Somomyia rectinervis*, *S. rufigena*, and *S. rupicola*. *Lucilia regina* Meig. is the type

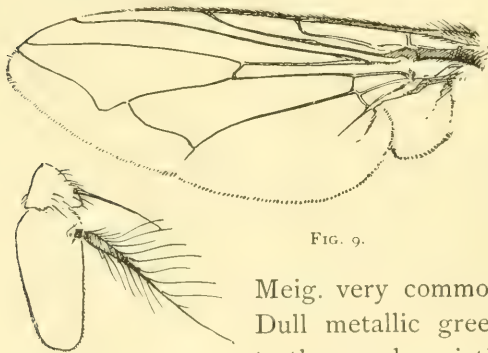


FIG. 9.

I the genus *Phormia* Desv. *L. terraenovae* Desv. is *Phormia groenlandica* Zett., and Desvoidy's name has priority (perhaps this is *P. caerulea* Desv.).

*Phormia*.—*P. regina*

Meig. very common everywhere (Fig. 9). Dull metallic green usually, but subject to the usual variations of metallic-colored

Calliphorinae; legs black; prostigma red to yellow; antennae pale brown to black; frontal vitta pale brown to black; palpi red to yellow; squamulae naked, white to yellowish brown. Front of male very narrow, of female about one-third as wide as head. This species seems to be rare in Europe. I am

indebted to Mr. V. von Roeder for a pair which has enabled me to be certain of the identity of the American specimens.

*P. terrae-novae* Desv., Fig. 10 (*Musca groenlandica* Zett.).—Common. Metallic blackish blue, with black legs and blackish

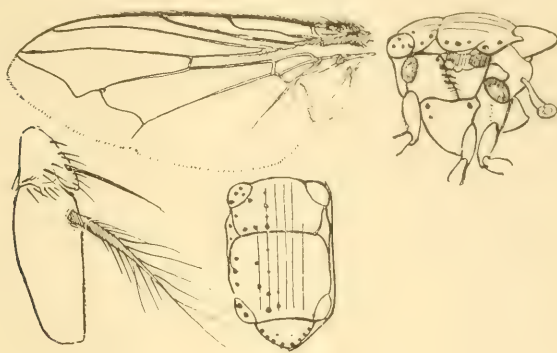


FIG. 10.

squamulae. Squamula alaris hairy on its dorsal surface, *i.e.*, surface which is dorsal when the wings are closed. No distinct achrosticals cephalad the suture; usually four anterior dorso-centrals, of which the first and third are much larger than the

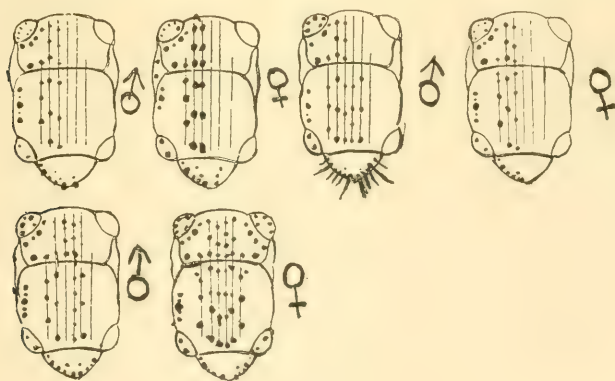


FIG. 11.

others. Front of male about one-eighth, of female one-third as wide as head. Prostigma black, palpi red, antennae black.

*Protocalliphora*.—*P. azurca* Fall. (Fig. 11) and *P. chrysorrhoea* Fall.—Very rare. The males are metallic bluish green, with





black head, antennae, and legs; palpi yellow at base, and brown or black toward apex, the relative amount of black varying much in different specimens. In *azurea* the antennae are inserted at the middle, in *chrysorrhoea* ventrad the middle of the head; the front of *azurea* is only half as broad as that of *chrysorrhoea*. The female of *chrysorrhoea* resembles the male, except for the usual sexual differences. The female of *azurea* is golden green, the thorax thickly white pollinose and with three blackish stripes, the abdomen whitish pollinose in certain lights. Front broad. I have compared my American with European specimens from Prof. G. Strobl and Dr. O. Schmiedeknecht.

## THE ACCESSORY BLADDERS OF THE TESTUDINATA.

FRANK W. PICKEL.

*Historical.* — More than a century ago Von Perrault (14) mentioned the occurrence of two coecal sacs, emptying into the cloaca in turtles. Later these sacs were drawn and described by Bojanus (4) in *Emys europaea* Schweigg. (*Emys orbicularis* Boulenger), and subsequently an account of them was published by Lesueur (10). According to the latter author these sacs, or bladders, which are very large, exceeding when expanded the bladder proper, are present in neither land nor sea turtles. They are also wanting, according to Lesueur, in the *Trionychidae*. He found them in twelve American species of *Emydidæ*, and in two species of *Chelydridæ*, namely, in *Chelydra serpentina* and *Chelydra lacertina* Schweigg. (*Chelydra lacertina* Boulenger). Bibron and Dumeril (3) and Schweigger, as well as Strauch, found them in *Chelydra lacertina* Schweigg. Lesueur (10) called these bladders "lumbar vessels or auxiliaries." Duvernoy (7) believed that they are only in part comparable with the "glandulae anales" of carnivorous mammals. He says: "This comparison is permissible on account of the shape and position, and perhaps in accordance with the plan of general composition of the whole organism, but is not admissible when a comparison of the details of their structure and their function is made; they are by no means organs with glandular walls forming a reservoir for secreted fluid." According to Duvernoy these bladders, to which he gives the name "accessory vessels," are very large, and the expansion of either of them equals that of the bladder alone. Their form is oval or cylindrical, and their position such that they must become compressed by the muscles of the lower belly, and may also be compressed by the posterior extremities, when the animal withdraws these into its carapace. M. Lesueur (10) found that

by blowing air into the living animal through the cloaca he could enlarge these vessels so much that they compelled the animal to project its extremities from its carapace and spread them out. The wall of the bladders is, according to Duvernoy (7), very thin, and is composed of two layers — an outer peritoneal layer, which is very rich in blood vessels, and an inner mucous membrane. He did not detect muscle fibers. He ascribes to these bladders a most peculiar function: “the animal can fill them with water, perhaps also with air, and can make use of them in diminishing its specific gravity. Hence we can explain why they are not found in land tortoises, which are not aquatic animals, and why they are absent even in the sea turtles, since the bodies of the animals are broad and flattened, and their extremities transformed into pinnate feet, and since, moreover, the specific gravity of sea water is greater than that of fresh water, they can dispense with the means of floating.”

It is even comprehensible, as Duvernoy (7) shows, that they should be absent in *Trionychidae*. In these turtles the extremities form strong rudders, as in the *Emydidae*, and their bodies are broad and flattened, thus enabling them to swim and float with ease. Lesueur (10) states that in *Cistudo carolina* (*Terrapene carolina* Linné, according to Strauch) these bladders are very small, and Duvernoy (7) concludes from this statement that their manner of living is the mean between that of the land turtles and the *Emydidae*. Stannius (16) merely says of these bladders, that, at least in the families *Testudinidae* and *Emydidae*, a pair of sacs open into the cloaca. Owen (13), who calls them “cloacal sacculi,” considers them to be only transitory structures. Budge (5) critically examined them in *Cistudo amboinensis* Gray (*Terrapene amboinensis* Daudin, according to Strauch) (*Cyclemis amboinensis* Boulenger), and found them in both sexes. He calls them “anal bladders.” They consist of two membranes; the peritoneum appears to make up only the outer surface of the organ; and next to the posterior part of the bladder wall he finds an oblique striated muscle, which proceeds from the carapace and extends nearly up to the muscular cloaca. Here it becomes sinewy and forms a ligament, which

partly unites with that of the other side, partly diverges to the tendinous ligament which is seen in the middle line of the cloaca. The peritoneal covering continues over on to the anal bladders and unites, by means of a fold, with the part of the peritoneum which overspreads the posterior surface of the bladder. By means of the two membranous expansions before and behind, each bladder becomes surrounded as with a loop which must draw itself together as soon as the above-mentioned muscle contracts. According to Budge (5) it is very improbable that these "anal bladders" are true bladders and serve for the reception of urine. The true bladder has the shape and structure of the homologous organ in other vertebrates, but the "anal bladders," as Budge (5) shows, seem not to possess anything like a muscle sheath. As we have seen, Stannius (16), in opposition to Duvernoy, states that the "Bursae anales" are not only found in the *Emydidæ*, but also in the land tortoises. In the *Emydidæ* Hoffman (9) found them in the male as well as in the female of *Clemmys* and *Emys*. He examined these bladders and distinguished in them three layers — a peritoneal layer, a muscle-fiber layer, and a mucous membrane. The muscle-fiber layer is very strongly developed and permits great expansion and vigorous contraction. He says: "What the function of these bladders may be has remained entirely unknown to me." According to him they are wanting in the sea turtles, *Chelonia imbricata* Schweigg. (*Chelone imbricata* Boulenger) and *Chelonia viridis* Temm and Schleg (*Chelone mydas* Boulenger). In the *Chelydidæ* he found them in *Chelomys victoria* Gray (*Emydura krefftii* Boulenger), *Chelodina longicollis*, and *Chelys fimbriata*. In the last-named species they are very large and very thin-walled.

Of the *Trionychidæ* he examined a male of *Trionyx acgyptiacus* Geoffr. and a female of *Trionyx sinensis*. The "accessory bladders" were present in the male of *Trionyx acgyptiacus* Geoffr. (*Trionyx triunguis* Boulenger), and were distinguished by their unusually thin walls, as in *Chelys fimbriata*. They were not present in the female of *Trionyx sinensis* Wiegman. He says the occurrence of these "anal bladders" in the *Trionychidæ* shows that the view of Duvernoy is incorrect.

In *Testudo graeca* the "anal bladders" are wanting, at least in the male. He does not say whether they are present or not in the female, as he had no opportunity to examine a female specimen.

Rathke (15) claims to have found the so-called "after bladders" (Bursae anales), which, like the bladder, empty into the cloaca, only in *Emys europaea* Schweigger (*Emys orbicularis* Boulenger) and *Emys lutaria* Schweigger (*Emys orbicularis* Boulenger). In the young animals they were, as regards size, like the bladder in the adult.

In my own investigations I endeavored to secure species of as many different families of *Testudinata* as possible, and these distributed over a wide area. I examined in all thirty animals, representing sixteen species, ten genera, and five families. The fresh material was obtained in the vicinity of Chicago and from Connecticut, Georgia, and Mississippi. I also had the use of preserved specimens which were collected in Australia by Dr. Semon, of Jena, Germany, and sent to the late Dr. Baur, Associate Professor of Paleontology in the University of Chicago.

I have followed Boulenger's classification and nomenclature except for the American box tortoises. In mentioning species of this genus I have used Dr. Baur's terminology.

This work was done in Hull Zoölogical Laboratory under the direction of Dr. W. M. Wheeler, to whom I acknowledge my great indebtedness for valuable criticisms and suggestions.

I found large "accessory bladders" in both sexes of the following North American species: *Chelydra serpentina*, *Chrysemis picta*, *C. rubriventris*, *Malacoclemmys terrapen*, *Clemmys insculpta*, *Clemmys guttata*, *Emys blandingii*.

The following Asiatic and Australian species possessed large "anal bladders": *Cyclemis dhor* ♀, *Cyclemis amboinensis* ♀, *Clemmys japonica* ♀, *Chelodina longicollis* ♀, *Emydura krefftii* ♀, *Emydura latisternum* ♀.

The North American species, *Terrapene carolina*, ♂ and ♀, and *Terrapene triunguis*, ♂ and ♀, have very small "accessory bladders." In the latter, which had never before been examined, I found very rudimentary "accessory bladders" much



smaller than those of *T. carolina*. In both species the size and appearance of these bladders indicate that they have become functionless.

In general it may be said that the "accessory bladders" are large oval or cylindrical sacs, opening dorsally on each side of the cloaca, near its anterior end. They lie in the pelvic region and extend into the peritoneal cavity, covered by the peritoneum. In some species the lungs are in contact with a large portion of their upper surfaces. By means of a fold which comes between their openings, a part of the cloaca in front of them can be closed off, so that the bladders may communicate directly with the cloaca, thus completely excluding all the other openings except the anus. In many of the fresh specimens these bladders were found to contain a clear liquid. When empty their external surface is corrugated like that of the true bladder, and their internal mucous membrane is thrown into folds.



FIG. 1. — External dorsal view of the cloaca of *Terrapene carolina*, showing the size of the accessory bladders.

In regard to the minute structure of the "accessory bladders" the following data may be given: The "accessory bladders" have a muscular wall lined with a mucous membrane and covered with a serous coat. The muscular coat is made up of three layers, the inmost being incomplete. The principal fibers are longitudinal and circular, and the latter are arranged in bundles. Sections of the bladder and "accessory bladders" of *Chrysemis picta*, *Chelydra serpentina*, and *Emys blandingii* were made and compared. The mucous membrane is lined with epithelial cells which are arranged in layers. The cylindrical cells in the upper layer are very long and narrow. They gradually become more slender below, and again show expansions where the nuclei lie. The protoplasm of these cells is very finely granular. Three to four rows of round cells lie between the narrow projections of the cylindrical cells. The mucous membrane of the bladder is lined with epithelial cells which have a structure and arrangement similar to that of the

cells in the "accessory bladders." This similarity is best seen in camera lucida drawings of sections of the bladder and of the "accessory bladders."

#### THE FUNCTION OF THE ACCESSORY BLADDERS.

As is well known, the habitat of the group of animals called *Testudinata* is diversified. Some species are exclusively terrestrial, others are more or less amphibious, and still others

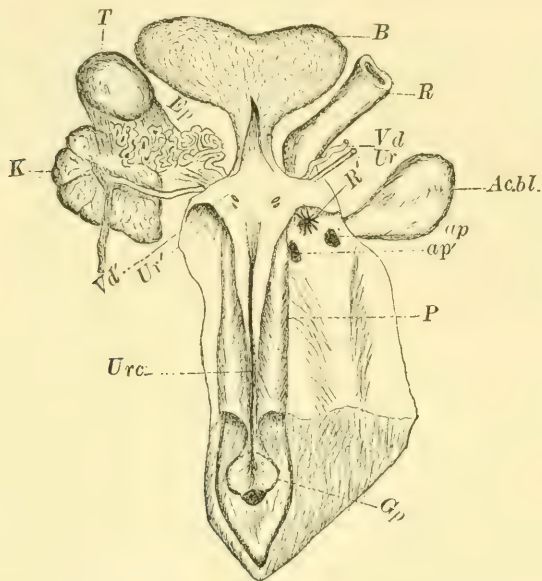


FIG. 2.—Male Urinogenital Organs of *Emys blandingii*. — K., kidney; Ur., ureter; Ur', aperture of ureter into the cloaca (cl.); B., urinary bladder; R., rectum; R', opening of rectum into the cloaca; Ac. bl., accessory bladder; ap. and ap', apertures of the accessory bladders into the cloaca; T., testis; Ep., epididymis; Vd., vas deferens; Vd. and Vd', openings of the vasa deferentia into the cloaca; Gp., glans penis; Urc., urinogenital canal; P., penis.

are aquatic. The presence or absence of "accessory bladders" in these animals appears to be, in a measure, correlated with their habits and environments. Lesueur (10) found that the "accessory bladders" were not present in land tortoises. I, too, have found these organs very small or entirely absent in the land species which I have examined (*Testudo polyphemus*, *Terrapene carolina*, and *Terrapene triunguis*).

C. Müller (12), who had frequent opportunities of observing

box tortoises in freedom as well as in captivity, found that they exhibited great aversion for water when placed in it, and always quitted it as quickly as possible. I have also observed that *Terrapene*, which is a decidedly terrestrial Emydid and has very rudimental "accessory bladders," is very uneasy when placed in water. It is generally believed that they never seek water but live wholly on vegetable matter, and obtain sufficient

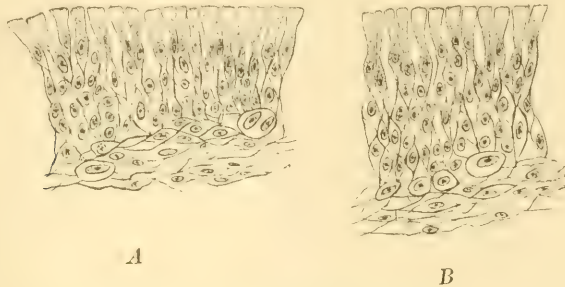


FIG. 3.—Sections through the bladder (A) and the accessory bladder (B) of *Emys blandingii*, showing the epithelial lining of these organs.

water from this source to maintain life. It would seem that the terrestrial mode of life of these tortoises may be an important factor in leading to a disappearance of the "accessory bladders."

Lesueur (10) again states that the "accessory bladders" are wanting in the *Cheloniidae* and *Trionychidae*.

Hoffman (9), too, says they are not present in the *Cheloniidae*, but are found in the *Chelydidae*. He claims they are present in one species of the *Trionychidae*, but this seems doubtful since no other investigator is found to support this statement. As before stated, I have examined several species of aquatic families, *Cinosternidae*, *Trionychidae*, and *Chelydidae*, and have found no "accessory bladders" in species of the first two families, but they were well developed in three species of the last.

The *Cinosternidae* and *Trionychidae* are purely aquatic and carnivorous in habit, and rarely go on land except to deposit their eggs in the sand on the shore near the water's edge.

I quote the following remarks concerning the *Chelydidae* from a letter received from Dr. Richard Semon: "*Chelodina*

*longicollis*, *Emydura krefftii*, and *Emydura latisternum* were all observed and caught by me in the Burnette River in Australia. They were taken in the middle course of the river. All three species live in those portions of the river where the water runs more slowly, and where the water plants are most abundant, in the so-called 'water holes' of the colonists. They are exclusively carnivorous, their diet consisting of all kinds of water animals. All three species are very rapacious. They often snatched the bait from the hooks which I had left dan-

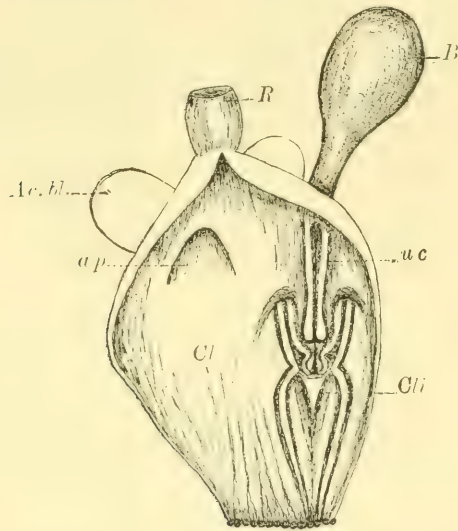


FIG. 4 shows in part the urinogenital organs of a young female *Chelodina longicollis*. — *R.*, rectum; *B.*, bladder; *Ac. bl.*, accessory bladders with a common aperture, *ap.*; *u. c.*, deep urinogenital canal; *Cli.*, clitoris; *Cl.*, cloaca.

gling in the water or on the bottom. I have rarely seen the animals on land. When disturbed *Chelodina longicollis* does not draw its head back straight in under the carapace, but folds it over to one side."

W. A. Haswell (8) found that the turtles of genus *Chelodina* have the habit of lying on the bottom of rivers and of drinking and then ejecting the water.

H. T. McCooen (11) states that the female of the genus *Chelodina* often goes a distance of three hundred meters on land to lay her eggs. She carries at least half a liter of water

and discharges it at intervals to soften the ground, that she may dig a hole about 18 cm. deep for her eggs. If this is not sufficient, she brings a second supply of water next morning and continues digging. The above account suggests that this genus may be amphibious in habit, and when more is known concerning the habits of the other genera of this family, they too may be found to be amphibious. The amphibious turtles, as their name implies, spend a part of their time on land, and often make considerable overland trips from stream to stream and from pond to pond in search of their food, which is both vegetable and animal, or in search of a suitable place to deposit their eggs.

Agassiz (1) says that "turtles (especially land and fresh-water turtles), like frogs, usually carry with themselves a quantity of water in the cloaca." According to the observations of Prof. J. Wyman (18) this water is taken up through the anus.

Anderson (1) says that some *Chelonia* draw in and eject water from the cloaca. In different species of the Southern Asiatic *Emydidæ* he often found the cloaca dilated with water, which they ejected in jets when they drew in their limbs and tail, as they usually do when suddenly taken from the water. He made an examination, immediately after death, of about one hundred specimens of this family which has "accessory bladders," but in no case did he find the organs distended with water. My own observations were made immediately after the death of the animals, and, as I have before stated, I found a liquid in the "accessory bladders" of *Emys blandingii*, *Chelydra serpentina*, and *Chrysemis picta*.

Darwin (6), speaking of the *Testudo nigrita*<sup>1</sup> of the Galapagos Islands, says :

"It is pretty well ascertained that the bladders of frogs serve as a reservoir in which to carry the moisture necessary to their existence. This function may be ascribed to these turtles. When killed some days after their visit to the springs of the island, the bladders were found distended with stored up liquid. The inhabitants, if thirsty while in the low grounds,

<sup>1</sup> This species of tortoise has no "accessory bladders."



use this condition to their advantage. They kill a turtle and drink the contents of the bladder." He (Darwin) saw one dead in which the liquid was clear and had a slight brackish taste.

The following observations on the Galapagos turtles I take from Dr. Baur's article in the *American Naturalist* (1889):—

"Porter, in his general description of the Galapagos tortoises, says: 'They require no provisions or water for a year, nor is any further attention to them necessary than that their shells should be preserved unbroken (p. 214). They carry with them a constant supply of water in a bag at the base of the neck, which contains about two gallons; and on testing that found in those we killed on board, it proved perfectly fresh and sweet.' In regard to the bag of water, Porter gives another statement (p. 100). He partly ascended a hill on Charles Island, and on his way back he found a large tortoise. 'It was opened with the hope of finding some water to allay our thirst. But we were disappointed,' says he, 'in only finding a few gills of a disagreeable-tasted liquid.' The tortoises taken in James Island had in their stomach or reservoir from one to two gallons of a 'taste by no means disagreeable.' It seems, therefore, that this 'water reservoir' is not always filled. Captain Benjamin Morrell, who visited the islands in 1825, says: 'I have had these animals on board my own vessels from five to six months without their once taking food or water; and on killing them I have found more than a quart of sweet fresh water in the receptacle which nature has furnished them for this purpose!'"

Townson (17) experimented with *Emys europaea* by placing the animal in colored water and then in clear water, and saw the colored water returned through the cloaca. He says: "Without doubt this colored water was taken into the 'accessory bladders.'" I have made several experiments with *Chrysemis picta* similar to that recorded by Townson, but I did not find any indication that the colored water was taken in through the cloaca and then ejected from it. I also made post-mortem examinations of each animal and found no trace of colored water in the "accessory bladders." The fact that Townson used in his experiment turtles of a different genus from the one which I used may explain the difference in our results.

These circumstances suggest that these "anal bladders" are related to the habits of the animals which have them, for in considering their distribution, as shown by these observations, it is plain that they are restricted to turtles which are semi-terrestrial and semi-aquatic, and those forms which are exclusively terrestrial and those which are exclusively aquatic do not possess them. And it would appear that it is due to the presence of these bladders in amphibious turtles like *Chrysemis picta* and *Emys blandingii*, that they can live under more varied conditions than such terrestrial and aquatic forms as *Terrapene carolina* and *Cinosternum odoratum*, for apart from these "anal bladders," there is no very great difference between the general structure of an *Emys* and a *Terrapene*.

From my own observations I conclude that the "accessory bladders" of *Testudinata* function as reservoirs or receptacles for liquid stored up for the use of the animal.

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HULL ZOÖLOGICAL LABORATORY,  
 UNIVERSITY OF CHICAGO,  
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